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Disturbed Alpine Ecosystems: Seedling Establishment of Early and Late Seral Dominant Species

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DISTURBED ALPINE ECOSYSTEMS: SEEDLING ESTABLISHMENT OF EARLY AND LATE SERAL DOMINANT SPECIES

by

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ABSTRACT

Disturbed Alpine Ecosystems: Seedling Establishment of Early and Late Seral Dominant Species

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This study examined the effects of seedbed and seedling environment on establishment of early and late seral dominant alpine species. Species studied included late seral dominant forbs (Geum rossii, Artemisia scopulorum, and Polemonium viscosum), early seral dominant forbs (Potentilla diversifolia and Sibbaldia procumbens), a late seral dominant grass (Festuca idahoensis), and early seral dominant grasses (Calamagrostis purpurascens and Deschampsia cespitosa). Germination responses of each species to wet vs. dry cold stratification and light vs. dark conditions were investigated. No statistical differences were observed in the seed germination of early and late seral dominant forbs or early and late seral dominant grasses, but significant differences were observed in the responses of grasses and forbs. Seed germination of forbs was greater under light than dark conditions and following wet cold storage.

Effects of fertilization on growth responses and nutrient uptake of G. rossii and D. cespitosa were evaluated in a factorial greenhouse experiment in which seedlings of each species were grown at four

levels of nitrogen (N) and phosphorous (P). The late seral dominant forb responded more like a species from a low-nutrient environment exhibiting lower relative growth rates, higher root:shoot ratios, and a smaller response to N than the early seral dominant.

A field experiment on the Beartooth Plateau, Montana, examined the soil environment and seedling emergence, growth, and survival of seeded early and late seral dominants on loamy sand soils of a severe disturbance and on peat soils of an undisturbed area during two growing seasons. Effects of fertilizer and mulch were examined on the severely disturbed area. Differences between uncleared turf and turf cleared of vegetation (gap disturbance) were evaluated on the undisturbed area. The gap disturbance had higher levels of N and P and warmer soil than the severe disturbance or vegetated undisturbed area. Soil water potentials were never low enough to result in plant stress. Seedling growth was slow - .005 g to .04 g dry weight the first growing season and .02 g to .20 g the second growing season. Growth was greatest on the gap disturbance and on fertilized plots of the severely disturbed area. Early seral dominants had the largest seedlings and the smallest R/R+S ratios. Mortality was low - odds of .50 were rarely exceeded even after two years. Survival was higher on warm, nutrient rich soils of the gap disturbance. Mulch increased emergence and survival on the severe disturbance. Fertilization increased mortality, probably because an initial pulse of N was followed by a rapid decline. Higher mortality occurred in 1986 than 1985 as 1986 had a shorter growing season and cooler air and soil temperatures early in the growing season.

(148 pages)

CHAPTER I

INTRODUCTION

Seedling establishment in disturbed alpine ecosystems is a relatively rare event when compared to seedling establishment in more temperate environments. Alpine ecosystems are characterized by growing seasons of only 60 to 90 days (Billings and Mooney 1968), growing season temperatures that average about 8°C, and temperatures during the growing season that may fall below 0°C (Marr and Willard 1970). Despite substantial annual precipitation, e.g., 63 cm on Niwot Ridge in Colorado (Billings and Mooney 1968) and 120 cm on the Beartooth Plateau in Montana (Brown et al. 1978), most water arrives as winter snow and soil drought is a common phenomenon late in the growing season. Wind is an omnipresent component of alpine environments and values as high as 5-8 m/s have been reported in the New Zealand alpine (Bliss 1985). Seedling establishment under these extreme environmental conditions is dependent upon the proper set of growing conditions and is frequently episodic.

Knowledge of seedling establishment in alpine ecosystems is restricted to observations of seedling survival under natural conditions (Osburn 1961, Brink 1964, Bonde 1968, Jolls and Bock 1983), seedling survival of selected species on different types of substrate (Bell and Bliss 1980), and general establishment of species used in seeding or transplant experiments (Harrington 1946, Selner and King 1977, Brown et al. 1978). Few quantitative data exist concerning the

factors that determine seedling establishment or differences in these factors among species.

Requirements for seed germination and seedling growth and survival are known to vary for species with different successional affinities (Grime 1977, 1979, Cooke 1979, Bazzaz 1983). Ruderal or early seral species are typical of severely disturbed but potentially productive environments, while competitive or late seral species dominate on productive, relatively undisturbed environments (Grime 1979). Successional processes in alpine ecosystems are less apparent than in more temperate systems (MacMahon 1980, 1981), but distinct successional sequences are frequently observed (Churchill and Hanson 1958, Bliss 1962, Webber and Ives 1978). Examination of early seral disturbed sites in the Beartooth Mountains, Montana, revealed that certain alpine species occur consistently and in higher abundances than other species on numerous types of alpine disturbances (Chambers et al. 1984). Based upon these observations and descriptions of late seral sites in the Beartooth Mountains (Johnson and Billings 1962), alpine species in this area can be categorized according to their successional affinity. Moderately competitive species that are frequent early colonizers but that exhibit wide geographic distributions and large ecological amplitudes are termed early seral dominants. Highly competitive species or late seral dominants are most often found in late seral ecosystems, but also colonize disturbed sites with suitable edaphic and topographic characteristics. Short-lived, rapidly growing species that are not competitive and that occur almost exclusively on disturbed sites are early seral ruderals.

The type of disturbance, including size, intensity, and frequency, determines the characteristics of the seedling environment, and consequently, the kinds of species that establish after any given disturbance (Grubb 1977, White 1979, Bazzaz 1983). Properties of the seedling environment that vary with disturbance type include physical soil characteristics (Chapin 1983), nutrient levels and mineralization rates (Vitousek et al. 1979, Vitousek 1985), and soil water potentials and temperatures (Vitousek 1985). In alpine ecosystems gap-type disturbances result from cryogenic soil movement (Johnson and Billings 1962) or small mammal burrowing and tunneling (Thorn 1982) that leave surface soil horizons in place. Soils are usually well-developed and highly organic. Severe disturbances are caused by geomorphological processes such as landslides and avalanches in which soil surface horizons are removed. Soils are often less well-developed and nutrient availability is low.

Several alternative models have been proposed to describe the mechanisms that determine the sequence of species colonization following disturbance. The facilitation model of Connell and Slatyer (1977) or relay floristics of Egler (1954) states that of those species arriving on a disturbed area only certain early successional species can establish. The early successional species then change the environment so that it becomes less suitable for recruitment of early seral species, but more suitable for recruitment of late seral species. This model is believed to be most applicable following a severe disturbance, such as a landslide or avalanche, in which surface soil layers are removed. In contrast, the tolerance model of Connell and Slatyer (1977) states that any species arriving on a disturbed

area that can survive there as adults can become established. Early colonizers modify the environment so that it is less suitable for recruitment of early seral species, but this does not affect subsequent recruitment of late seral species. This model is believed to apply following less severe or gap-type disturbances in which surface soil horizons are left in place. The degree to which either of these models applies in alpine ecosystems is largely unkown.

The purpose of this research was to examine the effects of disturbance type on seedbed and seedling environment, and consequently, on establishment of early and late seral dominant alpine species. To meet this objective, I performed greenhouse and laboratory experiments in Logan, Utah and a field study on the Beartooth Plateau, Montana. Chapter II describes a study that examined the laboratory germination responses of early and late seral dominant grasses and forbs to wet vs. dry cold stratification and light vs. dark conditions. Chapter III discusses a greenhouse study that estimated the range of growth responses and nutrient uptake characteristics of an early seral dominant alpine grass and a late seral dominant alpine forb to nitrogen and phosphorous availability. The field study was the major thrust of this research and is detailed in Chapter IV. In brief, the soil environment and seedling emergence, growth, and survival of early and late seral dominant alpine species on an undeveloped alpine soil typical of a severe disturbance were compared to those on a highly organic, well-developed soil representative of a gap-type disturbance. In addition to evaluating differences between the two types of areas, specific comparisons were made within each disturbance type. The severely disturbed area was

used to examine the effects of nutrient addition and mulching on the soil environment and on seedling emergence, growth, and survival. The undisturbed area was used to determine if differential establishment of early and late seral dominants would occur between native, uncleared turf and native turf cleared of vegetation.

The results of this study have implications for the reclamation of disturbed alpine ecosystems. Information about the germination characteristics of alpine species can be used to determine correct storage and seeding methods for seeds, while data about nutrient responses can indicate proper timing and application rates of fertilizer. Knowledge of the emergence, growth, and survival of species with different successional affinities on severe and gap-type disturbances can indicate appropriate species, soil amendments, and seeding techniques for different types of disturbances. The ability to include species with various life forms and successional affinities in reclamation efforts can increase species diversity, and ultimately, accelerate successional processes.

CHAPTER II

GERMINATION CHARACTERISTICS OF ALPINE GRASSES AND FORBS: A COMPARISON OF EARLY AND LATE SERAL DOMINANTS

INTRODUCTION

Knowledge of the germination characteristics of seeds of native species is important for establishing the desired plant community on disturbed lands. Most commonly, information about seed germination requirements is used to determine appropriate seed pretreatments (e.g., scarification or stratification) and methods of planting. Equally valuable is information concerning the potential of native species to recolonize a disturbed area, either from seeds present in replaced topsoil, sown on the area or dispersed from adjacent plant communities. In natural recolonization, the seeds and vegetative propagules present on the site at the time of disturbance constitute the "initial floristic composition" (Egler 1954) and can influence both the direction and rate of vegetation development (Connell and Slatyer 1977, MacMahon 1980, 1981). Seeds and other propagules initially present on a site may have greater influence on subsequent successional processes than immigrating disseminules due to earlier establishment and reproduction.

Many of the species commonly used in revegetation cannot survive and reproduce on disturbed alpine sites. Revegetation efforts in alpine areas have focused on native early seral dominant grasses primarily because of their high seed production and rapid growth characteristics

(Brown et al. 1978, Brown and Johnston 1979). Alpine sites reclaimed with early seral dominant grasses exhibit little change in species composition or invasion by other species even after 8 years (Brown et al. 1984). Inclusion of late seral dominant species in alpine revegetation may accelerate the rate of succession and facilitate the restoration of ecosystem functioning.

The germination responses of various perennial alpine species have been investigated with respect to temperature (Sayers and Ward 1966, Marchand and Roach 1980), light (Bliss 1958, Amen and Bonde 1964, Sayers and Ward 1966, Haggas et al. 1987), length of storage (Bonde 1965), scarification, stratification, leaching, extraction, and application of plant growth regulators (Amen and Bonde 1964). Seed germination responses of three annual alpine plants to light and stratification were evaluated with respect to the seed environment of the individual species' preferred habitat (Reynolds 1984). Only Marchand and Roach (1980) examined the reproductive characteristics of species from a particular successional state (viz., early seral dominants), and a consistent pattern of seed germination was not observed.

This study examined the germination responses of early and late seral dominant alpine forbs and grasses to conditions that seeds of these species were likely to experience in their native environment. In alpine areas early successional stages are frequently dominated by grass species while late successional stages are characterized by forb species (Chambers et al. 1984). These observations prompted two questions: (1) Do differences exist in the germination responses of early and late seral dominant alpine species to stratification and light that are independent of life form (grasses and forbs)? (2) Are there differences

in the germination response of grasses and forbs to stratification and light that are independent of successional stage?

METHODS

The species studied are broadly distributed throughout the central and southern Rocky Mountains and occur naturally on both early and late successional alpine sites within the Geum turf community (Johnson and Billings 1962, Chambers et al. 1984). They were chosen because of their successional affinity and potential for revegetation, e.g., large basal cover. The successional classification of early or late seral dominant was based on cluster analysis of species occurring on disturbed alpine sites in the Beartooth Mountains, Montana (Chambers et al. 1984) and on descriptions of late successional alpine communities in the same area (Johnson and Billings 1962). They included three late seral dominant forbs, Geum rossii (R. Br.) Ser., Artemisia scopulorum Gray, and Polemonium viscosum Nutt.; two early seral dominant forbs, Sibbaldia procumbens L. and Potentilla diversifolia Lehm.; one late seral dominant grass, Festuca idahoensis Elmer; and two early seral dominant grasses, Calamagrostis purpurascens R. Br. and Deschampsia cespitosa (L.) Beauv. It should be noted that D. cespitosa occurs as an early seral dominant on alpine disturbed sites, but is also a major component of the Deschampsia meadow vegetation type (Chambers et al. 1984).

Seeds were collected in September 1983 on the Beartooth Plateau, Montana (lat. 45°00' N, long. 109°30' W; elevation 3050 m). Seeds of late successional species were collected from undisturbed native sites, and seeds of early seral species were collected from disturbed early

seral sites. Following harvest, seeds were allowed to dry for 2 weeks before threshing and cleaning. Subsequent fanning removed light and unfilled seed, and the final product was stored dry at 1-2°C until initiation of the germination tests, 4 weeks later. Cold, dry storage more nearly approximated field condition than storage at some higher temperature.

Seed viability was evaluated using a 1% aqueous solution of 2, 3, 5 triphenyltetrazolium chloride (tetrazolium) (U.S. Department of Agriculture, 1974). Seeds were soaked in distilled water for 18 h, the seed coats were sliced with a razor, and the seeds were immersed in tetrazolium. After a 48-h dark incubation at 30°C, seeds with completely stained embryos were scored as viable. Three replications of 25 seeds of each species were used.

The germination study involved 90 days of dry cold storage or wet cold storage (stratification) treatment followed by germination in light or dark conditions with daytime temperatures of 18°C ± 1°C (14 h) and nighttime temperatures of 4°C ± 1°C (10 h). Three replications of 100 seeds of each of the eight species were used for each treatment. For the dry cold storage treatment, dry seeds were placed in a light-proof container in a cold chamber maintained at 1-2°C for 90 days. The wet cold storage treatment involved true stratification--i.e., each replication was inserted into an empty tea bag, placed in distilled water for 24 h imbibition, and put into an individual compartment of a saturated muslin sack. The muslin sack was then inserted between layers of saturated peat moss inside of a plastic bag and placed into a dark, cold chamber at 1-2°C. All seed manipulations were performed under a green safe-light.

After the 90-day cold storage treatment, seeds were removed from the cold chamber. Stratified seeds were extracted from the storage packets and all seeds that had germinated were recorded. Seeds that had received the dry cold storage treatment and ungerminated stratified seeds were scattered evenly over water-saturated alpine soil in 10 cm x 10 cm seed boxes. The alpine soil was a sandy loam with a pH of 7.1 that had been collected from a barrow pit on the Beartooth Plateau in the same area as the seed. A complete description of the soil is given in Chambers et al. (1987b).

Seed boxes were placed in two GCA Precision Scientific incubators; one for the dark treatment and one for the light treatment. The light-treated seeds received 14 h of light timed to coincide with the 18^{o}C temperature. Light was provided by 'cool-white' fluorescent bulbs located in the incubator door and was spatially nonuniform, ranging from 15 to 51 umol$\cdot$m$^{-2}\cdot$s^{-1}. Therefore, seed boxes were randomly positioned within the incubator and rerandomized every other day.

Seeds were examined for germination every second day for 32 days. A seed was considered to have germinated if either the radicle or cotyledon had emerged 1 mm beyond the seed coat. Dark-treated seeds were observed only under a green safe-light.

Major differences between species and treatments were examined with three-way analysis of variance (ANOVA) of the final germination percentages. Linear combinations of the interaction means were used to determine differences in species responses to treatments, and two-way ANOVA's were used to evaluate treatment differences within species. Comparisons of viability between species were performed with Fisher's Protected LSD. All percentage data were arcsine transformed. Rate of

germination was the number of days required for 50% of the final germination to be attained. Differences between treatments in the rate of germination were examined using Wilcoxon signed rank tests.

RESULTS

Seed viability

Viability percentages for the eight species ranged from 100% for P. diversifolia to 79% for C. purpurascens (Table II.1). There were no consistent differences between either successional affinity (early vs. late seral dominant) or life form (grass vs. forb).

Response to light and storage treatments

Only slight differences were observed in the germination responses of seeds of early and late seral dominant species to stratification and light, but clear differences emerged between responses of seeds of the grasses and forbs. All of the forbs, both early and late seral dominants, had significantly higher germination under light (vs. dark) conditions ($P < 0.01$ to $P < 0.001$), and germination was greater following wet cold storage (vs. dry cold storage) (S. procumbens $P < 0.05$; all others, $P < 0.01$) (Tables II.2 and II.3). All forbs except P. viscosum had significant interactions between storage and light treatments ($P < 0.05$ to $P < 0.01$). Wet cold storage was effective in promoting seed germination, but germination of wet cold stored seeds was less enhanced by light than was germination of dry seeds.

TABLE II.1. Seed viability of early and late seral dominant alpine species determined from a standard tetrazolium test.

Species	Mean(%)*	C.I.+	
Potentilla diversifolia	100	100-100	a++
Artemisia scopulorum	97	82-99	a b
Polemonium viscosum	96	77-99	a b
Geum rossii	93	88-97	b c
Festuca idahoensis	94	84-99	b c
Sibbaldia procumbens	83	62-97	c d
Deschampsia cespitosa	81	72-89	c d
Calamagrostis purpurascens	79	47-98	d

* Calculated from arcsine transformed data and back-transformed (n=3).

\+ Upper and lower 95% confidence limits calculated on arcsine transformed data and back-transformed. Interval is asymmetrical due to transformation.

++ Means having different designations are different at $P < 0.05$. Mean comparisons were made using Fisher's Protected LSD on arcsine transformed data (MS = 0.277, df = 16).

TABLE II.2. Germination response of early and late seral dominant alpine species to wet or dry cold storage and light (14 h day, 10 h night) or dark conditions with daytime termperatures of 18°C and nightime temperatures of 4°C.

	Dry cold storage				Wet cold storage			
	Light		Dark		Light		Dark	
	Mean(%)*	C.I.+	Mean(%)	C.I.	Mean(%)	C.I.	Mean(%)	C.I.
FORBS								
Late seral								
Geum rossii	100	93-98	30	23-38	99	89-97	90	81-96
Artemisia scopulorum	67	37-91	.6	.3-5	88	64-100	46	36-56
Polemonium viscosum	3	1-6	.1	.6-2	17	10-27	11	4-20
Early seral								
Sibbaldia procumbens	64	42-83	6	.1-21	61	32-86	34	24-46
Potentilla diversifolia	71	63-79	10	7-13	90	88-92	63	52-74
GRASSES								
Late seral								
Festuca idahoensis	93	81-99	91	88-93	86	84-88	88	69-98
Early seral								
Calamagrostis purpurascens	77	68-85	83	70-93	93	55-96	99	93-100
Deschampsia cespitosa	95	70-98	64	49-78	63	59-67	46	41-51

* Total mean germination of viable seeds (%) summed over 30 days. Values were calculated on arcsine transformed data and back-transformed (n = 3).

+ Upper and lower 95% confidence limits of total germination calculated on arcsine transformed data and back-transformed. Interval is asymmetrical due to transformation and does not always include mean.

TABLE II.3. Germination response of individual species to wet or dry cold storage (W) and light or dark conditions (L) as determined from two-way ANOVAs.

Species	Source	df	F	P*
FORBS				
Late seral				
Geum rossii	L	1	107.8	***
	W	1	33.5	***
	LxW	1	37.1	***
	Error	8		
Artemisia scopulorum	L	1	89.6	***
	W	1	41.5	***
	LxW	1	7.8	*
Polemonium viscosum	L	1	12.8	**
	W	1	64.1	***
	LxW	1	0.8	NS
	Error	8		
Early seral				
Sibbaldia procumbens	L	1	44.0	***
	W	1	6.0	*
	LxW	1	8.2	*
	Error	8		
Polemonium diversifolia	L	1	430.3	***
	W	1	298.3	***
	LxW	1	54.6	***
	Error	8		
GRASSES				
Late seral				
Festuca idahoensis	L	1	0.02	NS
	W	1	2.9	NS
	LxW	1	0.4	NS
	Error	8		
Early seral				
Calamagrostis purpurascens	L	1	2.2	NS
	W	1	11.4	**
	LxW	1	0.4	NS
	Error	8		
Deschampsia cespitosa	L	1	22.5	***
	W	1	24.7	***
	LxW	1	4.0	NS
	Error	8		

* Data are arcsine transformed. Significance levels: NS, $P > 0.05$; *, $P < 0.05$; **, $P < .01$; ***, $P < 0.001$.

In general, grasses responded less to treatments than forbs (Tables II.2 and II.3). F. idahoensis exhibited uniformly high germination for all treatments. C. purpurascens showed no significant response to light conditions, but wet cold storage resulted in significantly greater germination than did dry cold storage ($P < 0.05$). Germination of D. cespitosa was higher under light than dark conditions ($P < 0.001$), but contrary to the results for the forbs and C. purpurascens, germination was lower following wet cold treatment than dry cold treatment. No significant interaction between treatments was shown by any of the grasses.

Light had a greater effect on total seed germination than did storage treatment, but wet cold storage had a larger effect on the rate of germination. The number of days required for 50% of the final germination to be reached was significantly less following the wet cold storage treatment than the dry cold storage treatment for all species combined ($P < 0.01$; Fig. II.1, Table II.4).

Generally, light had no significant effect on the germination rate when compared with the appropriate dark treatment (Table II.4). Exceptions are the late seral dominant forbs, G. rossii and A. scopulorum, which required 2 to 3 times as long to reach 50% of the final germination under dark conditions than light conditions following dry cold storage. For these forbs, light enhanced both the total germination percentage and the rate of germination. P. viscosum, the other late seral dominant forb, required about twice as long to achieve 50% of the final germination under light conditions following dry cold storage. However, total germination percentages for this species were

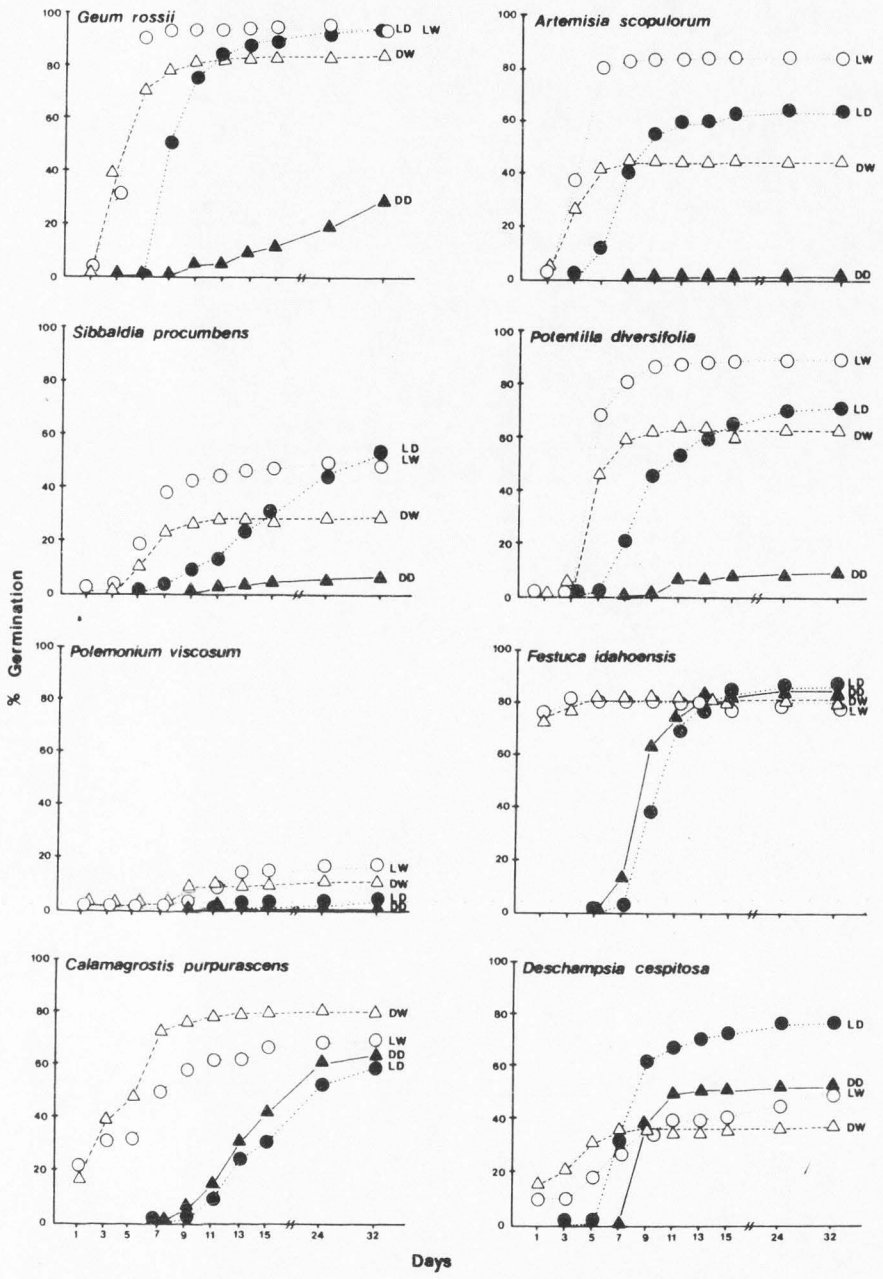

FIG. II.1. Germination response (total germination percentage) of early and late seral dominant alpine forbs and grasses over a 32-day period under light (L) or dark (D) conditions following wet (W) or dry (D) cold storage: LW, light/wet; LD, light/dark; DW, dark/wet; DD, dark/dry.

TABLE II.4. Days required for 50% of the final germination to be attained for early and late seral dominant alpine species in response to dry or wet cold storage and light or dark conditions.

	Dry cold storage		Wet cold storage	
	Light	Dark	Light	Dark
FORBS				
Late seral				
Geum rossii	7	2	5	5
Artemisia scopulorum	7	13	5	3
Polemonium viscosum	24	11	11	9
Early seral				
Sibbaldia procumbens	15	13	7	7
Potentilla diversifolia	9	11	5	5
GRASSES				
Late seral				
Festuca idahoensis	11	9	1	1
Early seral				
Calamagrostis purpurascens	15	15	7	5
Deschampsia cespitosa	9	9	7	3
Mean ± S.E.	12.1 ± 2.0	13.1 ± 1.7	6.0 ± 1.0	4.8 ± 0.9

low (3.3 in the light vs. 0.3 in the dark) and differences are probably not biologically meaningful.

Life form and successional relationships

There were no significant differences in the germination responses of the forbs G. rossii, A. scopulorum, S. procumbens, or P. diversifolia, although two are late and two are early seral dominant species (Table II.5). The response of P. viscosum was significantly different from the other late seral dominant forbs ($P < 0.05$ to $P < 0.001$) because of a small light enhancement effect and the magnitude of response to the wet cold treatment. P. viscosum's response was not significantly different from that of the grasses. However, dormancy was not broken for this species, and at this time the dormancy-breaking requirements are unknown. The late seral dominant forb, G. rossii, differed from all of the grasses in germination responses ($P < 0.01$ to $P < 0.001$), while the late seral dominant forb A. scopulorum differed only from the late seral dominant grass, F. idahoensis. This was due to the light enhancement effect in these forbs. The early seral dominant forb, S. procumbens, differed from the late seral dominant grass, F. idahoensis, but not from the early seral dominant grasses D. cespitosa and C. purpurascens. The responses of S. procumbens were intermediate between those of the late seral dominant forbs and the early seral dominant grasses.

TABLE II.5. Differences in germination response of early and late successional alpine species to dry or wet cold storage and light or dark conditions based on linear combinations of the interaction means (arcsine transformed); MS = 0.1045, df = 20.

	Species							
	Forbs					Grasses		
Species	GERO	ARSC	POVI	SIPR	PODI	FEID	CAPU	DECE
Forbs								
Late seral								
Geum rossii (GERO)	-	NS*	***	NS	NS	***	**	*
Artemisia scopulorum (ARSC)		-	*	NS	NS	*	NS	NS
Polemonium viscosum (POVI)			-	NS	NS	NS	NS	NS
Early seral								
Sibbaldia procumbens (SIPR)				-	NS	*	NS	NS
Potentilla diversifolia (PODI)					-	NS	NS	NS
Grasses								
Late seral								
Festuca idahoensis (FEID)						-	NS	NS
Early seral								
Calamagrostis purpurascens (CAPU)							-	NS
Deschampsia cespitosa (DECE)								-

* Significance levels: NS, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

DISCUSSION

Experimental limitations

Environmental control of seed germination in field situations may depend on interaction of factors not included in this study (Roberts 1981). Different species require differing amounts of temperature fluctuation for germination (Thompson et al. 1977), and variations in temperature can influence germination of grasses (Williams 1983b, Schonfeld and Chancellor 1983) and alpine species (Sayers and Ward 1966). The quality of light (e.g., red:far red ratio) can differentially influence the germination of seeds of different species (Smith 1973, Silvertown 1980) as can light intensity (Zimmerman 1977). Also, use of low-intensity green light to record seed germination of dark treated seeds may eventually result in germination of certain species (Grime and Jarvis 1975, Grime et al. 1981). Since all but two of the species studied exhibited 85% or greater germination of viable seeds for at least one treatment, we believe that the factors examined were appropriate for the objectives of this study.

Successional and life form implications

In this study, light increased total germination of forb seeds that had received either wet or dry cold storage. However, there were no differences in the germination responses of early and late seral dominants to light. In a survey of seed germination characteristics of 403 species from a wide range of habitats in the Sheffield area, Great

Britain, light promoted germination in most of the species examined (Grime et al. 1981).

An inhibitory effect of darkness was evident in many species that contribute to persistent seed banks, but such inhibition was also observed in species whose seeds are more transient in the soil. A specific comparison of early and late seral species showed that, with few exceptions, germination of the early seral forbs was much less under dark conditions than that of later seral grassland species (Grime and Jarvis 1975).

The ecological implications of seed germination characteristics of early and late seral dominant alpine species must be evaluated in the context of the unusual successional processes of this ecosystem. Few annual species exist in alpine ecosystems (Bliss 1971), and early colonizer species frequently persist in late seres (Muller 1952, Churchill and Hanson 1958). Vegetation is predominantly low-growing and dense, and reproduction within established stands is primarily vegetative via stolons or rhizomes (Bliss 1971). In this study, seeds of both early and late seral dominant forbs responded to light like seeds of typical early seral forbs in temperate systems. This light enhancement effect indicates that germination of both groups of forbs is benefitted by "gaps" in the community or disturbance.

The grass species in this study had less specific seed germination requirements than the forbs; these differences in final germination percentages were observed between different treatments. Seed germination studies of grassland species in Great Britain showed that germination of most indigenous grasses was initially high (Grime et al. 1981, Williams 1983a). In our study, the significantly greater

germination response of D. cespitosa to light was unique among the grasses and resembles the typical response of early seral species.

Light increased total percent seed germination more than wet cold storage, but wet cold storage significantly increased the rate of germination, especially for dark-treated seeds. This has important implications for both early and late seral dominant alpine species. Since alpine ecosystems are characterized by short growing seasons (Billings and Mooney 1968), a decrease in the number of days required for germination can increase the likelihood of plant establishment.

Revegetation recommendations

Results of this study have implications for the revegetation of disturbed alpine sites using these species. The light enhancement effect on seed germination observed in the majority of forb species indicates that seeds of these species should be sown on the soil surface. The increase in seed germination of most of the forb species following wet cold storage indicates that fall seeding of these species would maximize the opportunity for natural stratification. The less specific germination requirements of the grass species suggest that adequate field germination of these species could be obtained with a variety of seeding methods, e.g., surface sowing or shallow drilling. Successful establishment of D. cespitosa has been obtained by seeding with a seeder packer (Brown and Johnston 1979)--an implement that scatters the seed on the soil surface and presses it into the soil to different depths with a roller.

Seed germination information about early and late successional alpine grasses and forbs permits reclamationists to utilize methods that facilitate not only natural colonization of these species on disturbed areas, but also maximum seed germination when these species are seeded. Use of these species in seed mixtures can increase both the numbers of plant species and life history strategies on reclaimed areas, and thus help reclamationists meet legal requirements. Also, inclusion of late successional species may increase the rate of succession on reclaimed areas and allow more rapid restoration of ecosystem functioning.

CHAPTER III

RESPONSE OF AN EARLY SERAL DOMINANT ALPINE GRASS AND A LATE SERAL DOMINANT ALPINE FORB TO N AND P AVAILABILITY

INTRODUCTION

Nitrogen (N) and phosphorus (P) fertilization is a common cultural practice in the revegetation of disturbed alpine lands (Brown and Johnston 1979), yet little is known about growth responses or nutrient uptake characteristics of alpine species under varying levels of N and P availability. Species responses to N and P concentrations vary for P (Bradshaw et al. 1960, Rorison 1968, O'Connor et al.1972), N (Bradshaw et al. 1964), and both N and P (Pigott and Taylor 1964, Shaver and Chapin 1980). Knowledge of the responses of alpine species to N and P is important in determining effective revegetation techniques. In field situations, N and P additions can affect species establishment (Hertzog and Young 1983), competitive relationships, and ultimate stand composition (DePuit and Coenenberg 1979, Halvorson and Bauer 1984).

Response to N and P availability has been correlated with the soil nutrient status of the species' native environment (e.g., O'Connor et al. 1972). Changes in nutrient cycling and ecosystem nutrient budgets occur during succession (Vitousek and White 1981, Tilman 1982). Availability of nutrients, especially N, can be considerably higher early in secondary succession than later, depending upon the type of disturbance and stage of soil development (Vitousek et al. 1979, Tilman 1985). Typically,

species from early secondary successions with high nutrient availability exhibit rapid growth (Marks 1974, Grime and Hunt 1975), and have high rates of nutrient absorption (Chapin 1980). In contrast, species from soils with low nutrient availability have slower rates of growth and nutrient absorption and higher tissue nutrient concentrations (Chapin et al. 1982).

In general, patterns of nutrient absorption and allocation change as nutrient availability in the soil and species growth form and composition change during succession (Chapin 1983). In temperate ecosystems, short-lived, rapid-growing herbs with large reproductive allocations are generally replaced by longer-lived herbs and finally by slow-growing, long-lived species with large storage reserves and small reproductive output.

Alpine reclamation efforts have focused on early seral dominant grasses that exhibit high seed production and germinability and rapid establishment (Chambers et al. 1984). Attempts to establish late seral dominant species with early seral dominant grasses and with applied N and P have failed (Ray Brown, unpublished data). Successful establishment of late seral dominant species in alpine reclamation could accelerate successional processes, facilitate rapid restoration of ecosystem functioning, and return species diversity to premining levels - a legal requirement on many mine sites.

The objectives of this study were twofold: (1) to estimate the range of growth responses and uptake characteristics of an early seral dominant alpine grass and a late seral dominant alpine forb to N and P availability, and (2) to determine if the growth responses and N and P

uptake characteristics of these two taxa were consistent with those obtained for early and late successional species from other ecosystems.

METHODS

Soil for the experiment was collected from a gravel barrow pit on the Beartooth Plateau in Montana (45°00' N, 109°30' W, elevation 3200 m). The soil was selected to represent highly disturbed alpine soils of granitic origin that have had the high organic matter topsoil layer removed. Analysis (n = 5) of the collected soil was performed within 2 wk after the samples were collected. The experiment was initiated within 8 wk after the soil was collected. The soil was a sandy loam as determined from the hydrometer method (Day 1973) and the pH was 7.1 as measured with a glass electrode in a 1:1 slurry of soil and distilled water (McLean 1980). Organic matter was determined to be 0.13% using a chromic acid digestion with a colorimetric measurement of organic matter (Walkley and Black 1934, as modified by Schulte 1980.) Phosphorous was 6.7 mg/kg as measured with the Bray-1 procedure using the Fiske-Subbarrow reducing agent (Bray and Kurtz 1945, Laverty 1963, Knudson 1980). Levels of total, NO_3^-, and NH_4^+ nitrogen were 80.0, 7.3, and 3.3 mg N/kg, respectively. Total nitrogen was determined from micro-kjehldahl digestion (Bremner and Mulvaney 1982), NO_3^- was evaluated using a specific ion electrode in a saturated calcium sulfate extraction (Carson 1980), and NH_4^+ was measured from a 1 soil:2, 1 M KCl extraction and the Nessler reagent (Greweling and Peech 1960). The soil was sieved through a 1-cm screen and air dried (water content < 0.08%) before use.

The study was conducted in a greenhouse in Logan, Utah, USA, during February, March, and April of 1984. A factorial design was used with four levels of N (4.2, 38.8, 73.3 and 107.6 mg/kg), four levels of P (6.7, 39.5, 72.4 and 105.0 mg/kg), three replications of each treatment, and two plants per pot. Treatment levels are referred to hereafter as N1, N2, N3, N4 and P1, P2, P3, P4, respectively. The levels of N and P used in the study were calculated on an elemental basis and included amount of available N (NO_3^- and NH_4^+) and amount of available P (PO_4^{-3}). The lowest levels (N1 and P1) were the amounts that existed in the native alpine soil without nutrient addition. The highest levels (N4 and P4) included amount of available N and P present in the native alpine soils. The highest levels were similar to those used in nutrient uptake studies in arctic Eriophorum ecosystems (Tamm 1954, Shaver and Chapin 1980) and to the maximum levels applied to cropland in temperate regions (Tisdale and Nelson 1975).

The sources of N and P were NH_4NO_3 and $CaH_4(PO_4)_2$. Amounts of N and P for each treatment were calculated based on the weight of the air-dried alpine soil necessary to fill an individual pot, 11.0 cm in diameter and 14.5 cm tall. Equal weights of soil were used for each pot, and the soil was thoroughly mixed with the nutrients on an individual pot basis. N and P availability was not remeasured during the course of the study. Plant growth was extremely slow during the study, and because roots filled only a small portion of volume, it seemed unlikely that plant uptake had significantly decreased nutrient levels. In addition, the low levels of organic matter were indicative of low levels of mineralization.

Two circumboreal species were selected for study: (1) Deschampsia cespitosa (L.) Beauv., an early seral grass, and (2) Geum rossii (R.Br.)

Ser., a late seral forb. The early seral classification of D. cespitosa was based on a cluster analysis of early colonizer species on four, 20-to 30-year old disturbed alpine sites in the Beartooth Mountains (Chambers et al. 1984). In alpine ecosystems D. cespitosa is a dominant species on disturbed sites in the Geum turf community and in D. cespitosa meadows (Johnson and Billings 1962). Geum rossii was selected because it is a widespread dominant in the late successional stages of the Geum turf community (Johnson and Billings 1962).

Seeds were collected in September 1983 from the same general area that supplied the soil. Seeds of early seral species were collected from early successional sites and seeds of late seral species from late successional sites. Following harvest the seeds were dried, cleaned, and then stored at 0°C until use. Seedlings were established in seed boxes and transplanted into the treatment pots 4 wk after emergence. Pots were randomized within replications, and replication position on the greenhouse bench was changed weekly. The soil within an entire pot was watered with distilled water to approximately field capacity when the soil surface was dry to a depth of 1 cm. Surface watering was alternated with bottom-watering to prevent salt accumulation at any one location within the pot, and runoff water was poured back into the pot to reduce N and P loss.

Natural light was supplemented with fluorescent GRO lights and incandescent lights that provided a 14-h daylength. Maximum irradiance ranged from 279 W/m to 838 W/m daily. Temperature fluctuated from 18 to 26°C and relative humidity ranged from 15 to 40%.

Initial root and shoot weights of the seedlings were determined at the time of transplanting by harvesting 20 extra seedlings of each

species. The treatment plants were harvested 8 wk after transplanting. Roots and shoots of harvested plants were separated and roots were carefully washed. Dry weights of both roots and shoots were obtained after oven-drying at 78°C for 24 h.

Concentrations (%) of N and P in the shoots were determined for seedlings from the final harvest. Because a slow growth rate resulted in a low quantity of material for analysis, only N concentrations were obtained for G. rossii. Analyses were performed using mass spectrometry of oven-dried samples that had been ground with a Wiley mill. Content (g/plant) of N and P in the shoots was calculated as the product of shoot concentration and shoot weight.

Data analysis

Responses of the two species to the levels of N and P were evaluated by measuring final root and shoot weights, N and P concentrations and contents, and by calculating root:shoot (R:S) ratios, and relative growth rate (RGR):

$$RGR = (\ln W_t - \ln W_o)/t,$$

where W_o is the average dry weight of plants (roots plus shoots, g) at transplanting, W_t is the individual dry weight of the plants (roots plus shoots, g) at the end of the experiment, and t is the time interval (56 days).

Because of differences in the magnitude of the growth responses of G. rossii and D. cespitosa, comparisons between the species for root and shoot weights and R:S ratios were made from linear contrasts of the

interaction means. Analysis of variance was used to assess species differences in RGR and N concentration and content.

Level N4 resulted in high mortality of G. rossii, and so was excluded from all analyses involving this species. Because of the differences in response between the two species and the missing N level in G. rossii, differences between treatments were determined from separate analysis of variance for each species. Mean differences within treatments were examined with Fisher's Protected LSD.

The assumption of normality for the analyses of variance was validated from probability plots of the standardized residuals versus the normal scores. Proportional data were transformed using an arcsine function.

RESULTS

Growth responses

Significant differences existed in the responses of G. rossii and D. cespitosa to N and P for shoot and root weights and for R:S ratios (Fig. III.1; Table III.1). Shoot growth was significantly different over levels of N for G. rossii ($P < 0.05$) and D. cespitosa ($P < 0.001$). Over all levels of P, both species had significantly lower shoot growth for level N1 than for any other N level; however, increasing N above level N2 did not result in greater shoot growth. Level N4 resulted in high mortality of G. rossii indicating that the upper tolerance limit of this species had been exceeded. Significant differences in shoot growth also existed over levels of P for G. rossii and D. cespitosa ($P < 0.001$).

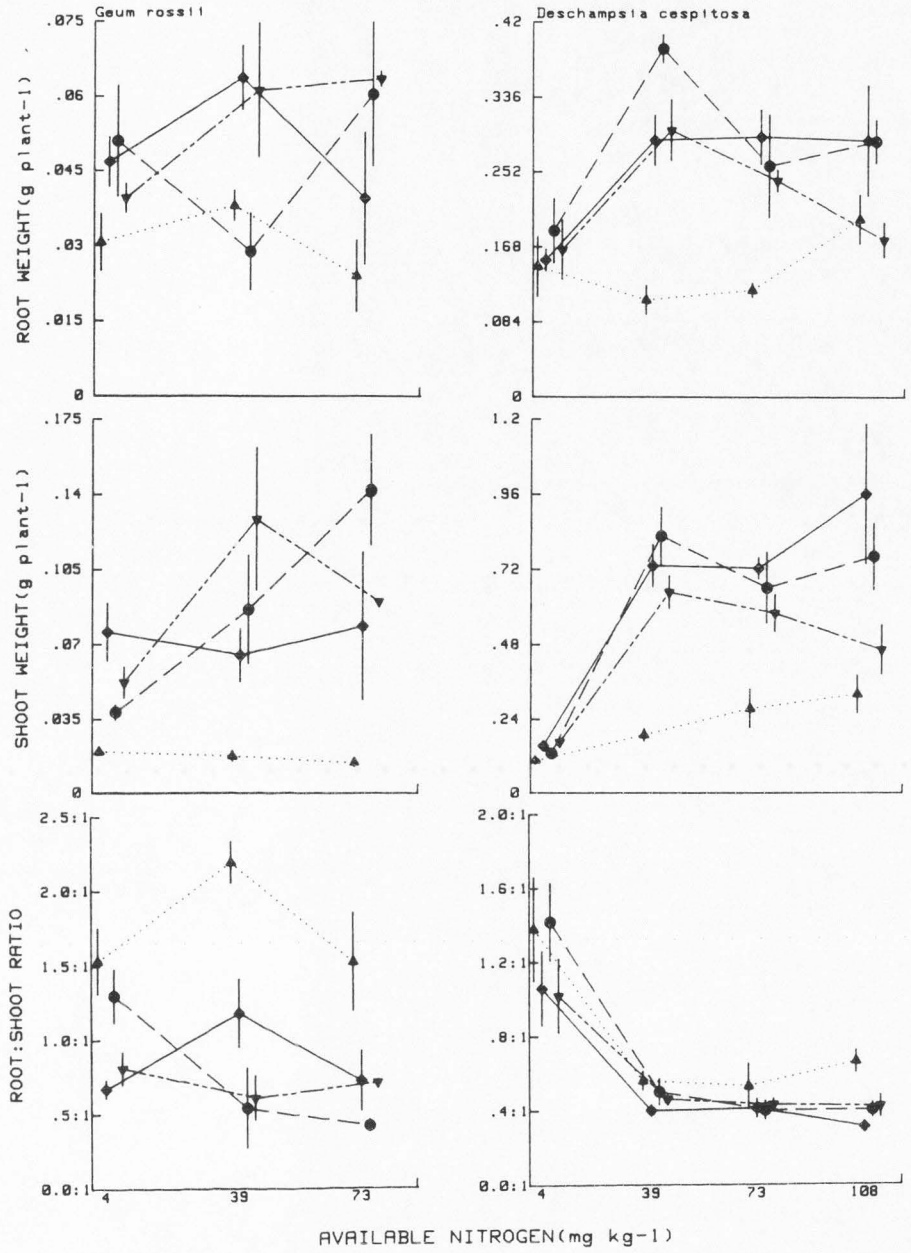

FIG. III.1. Mean shoot and root weights and R:S ratios of G. rossii and D. cespitosa seedlings grown for 8 weeks in a factorial experiment at four levels of available N (NH_4^+ plus NO_3^-) and P (PO_4^{-3}). Levels of P = 6.7 (▲), 39.5 (◆), 72.4 (●), and 105.0 (▼) mg/kg.

TABLE III.1. Results of individual ANOVAs and Fisher's protected LSDs comparing differences within species.

		Geum rossii		*Deschampsia cespitosa*	
Measurement	Factor	Significance level	Fisher's protected LSD	Significance level	Fisher's protected LSD
Shoot weights	N	*[*]	N1 N2 N3[+]	***	N1 N3 N2 N4
	P	***	P1 P2 P3 P4	***	P1 P4 P3 P2
	Rep	NS		NS	
	NP	*		***	
Root weights	N	NS		***	N1 N3 N4 N2
	P	NS		***	P1 P4 P2 P3
	Rep	NS		NS	
	NP	NS		**	
Root:shoot ratio	N	NS		***	N1 N2 N4 N3
	P	***	P1 P2 P3 P4	**	P1 P3 P4 P2
	Rep	NS		NS	
	NP	**		NS	
Relative growth rate	N	NS		***	N1 N3 N2 N4
	P	***	P1 P2 P3 P4	***	P1 P4 P3 P2
	Rep	NS		NS	
	NP	**		***	
N concentration	N	***	N1 N2 N3	***	N1 N2 N3 N4
	P	NS[++]		NS	
	Rep	NS		NS	
	NP	NS		NS	
N content	N	***	N1 N2 N3	***	N1 N2 N3 N4
	P	NS[++]		***	P1 P4 P3 P2
	Rep	NS		NS	
	NP	NS		*	
P concentration	N			***	N1 N2 N3 N4
	P			***	P1 P2 P3 P4
	Rep			NS	
	NP			NS	
P content	N			NS	
	P			**	P1 P2 P3 P4
	Rep			NS	
	NP			NS	

[*] NS, P > 0.05; *, P < 0.05;**, P < 0.01;***, P < 0.001.

[+] Means shown without the same underline are different at the P < 0.05 level.

[++] Includes levels P2, P3, and P4 only.

Lower shoot weights were found for level P1 than for other levels of P in both species. For D. cespitosa, level P4 resulted in greater shoot growth than level P1, but less growth than levels P2 and P3. The decline in shoot growth of D. cespitosa at level P4 resulted in a significant N/P interaction.

Root weights showed no significant differences over levels of N or P for G. rossii (Fig. III.1; Table III.1). In contrast, differences in root weights were observed for D. cespitosa over levels of both N and P ($P < 0.001$). Less root growth occurred at level N1 than at other levels of N. Also, root weights at level P1 were lower than at other P levels. Decreased root growth at level P4 and at high levels of N resulted in a significant N/P interaction.

R:S ratios were higher for G. rossii than D. cespitosa for all treatments except the lowest level of N across all levels of P. For G. rossii there were no differences among N levels, but highly significant differences among P levels ($P < 0.001$). Differences among P levels were due to a higher R:S ratio for level P1 than for other levels of P. R:S ratios decreased at the highest levels of P (P3 and P4) for levels N2 and N3, while R:S increased for the lowest levels of P. This resulted in a significant N/P interaction for G. rossii. D. cespitosa showed large differences in R:S ratios over levels of N ($P < 0.001$) but lesser differences over levels of P ($P < 0.01$). The differences among N levels for D. cespitosa resulted from a high R:S ratio in level N1, but the differences among P levels were less distinct. In this experiment, N was the primary factor regulating R:S ratio for D. cespitosa, while P was the controlling factor for G. rossii. For both species, the change

between high and low R:S ratios occurred at relatively low levels of N (4.2 - 38.8 mg/kg) and P (6.7 - 39.5 mg/kg).

In certain species the relative growth of roots and shoots depends on the size of the individual plant (Ledig et al. 1970, Long 1978). To determine if differences in R:S ratios were related to differences in the size of the plants, and not treatments, regressions of the natural logarithm of root weight against the natural logarithm of shoot weight were performed. Results of the regressions were consistent among treatments, indicating that differences between treatments were a function of the treatments themselves and not of an allometric relationship between relative root and shoot growth and plant size.

RGR of G. rossii was 45% - 75% that of D. cespitosa (Fig. III.2) despite slightly larger initial seedling weights for G. rossii (.0047 g/plant versus .0039 g/plant for D. cespitosa). Level of N had no statistically significant effect on the RGR of G. rossii (Table III.1). However, significant differences existed in P levels due to a low RGR associated with P1 ($P < 0.001$). RGR of D. cespitosa varied over levels of N ($P < 0.001$) and P ($P < 0.001$). For D. cespitosa, these findings are similar to those for shoot and root weights. In contrast, results obtained for G. rossii reflect the slightly greater response in shoot growth to P and the dependence of the R:S ratio on P. However, for both species, RGRs were affected by levels of N and P as indicated by significant N/P interaction terms.

N and P concentrations and contents

The small size of G. rossii plants grown at level P1 prevented

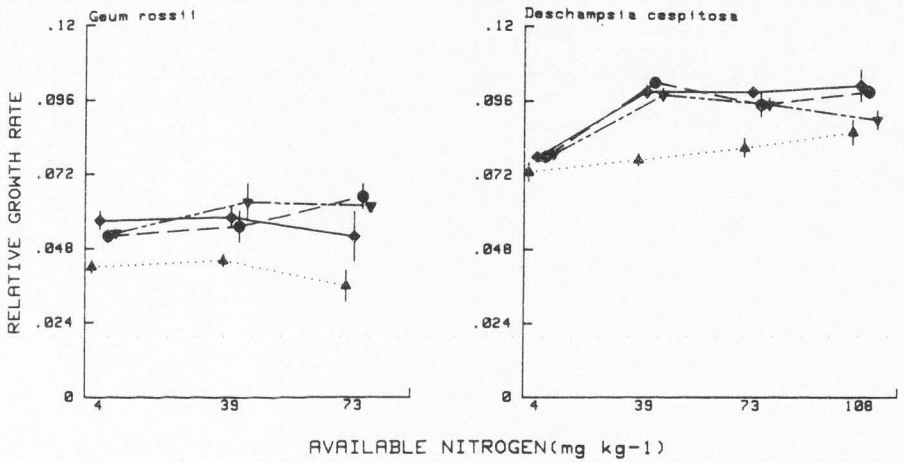

FIG. III.2. Mean relative growth rates of G. rossii and D. cespitosa grown for 8 weeks in a factorial experiment at four levels of N and P as in Fig. 1.

analyses of plant N concentrations for this level, except for P1N1. Therefore, comparisons of N concentration and content for G. rossii and between species were based on levels N1, N2, and N3, and P2, P3, and P4.

N concentration differed significantly between the two species ($P < 0.01$), although apparent similarities in the response to N and P levels existed (Figs. III.3 and III.4). N content varied to a greater extent between species ($P < 0.001$) than N concentration. N concentration of both species increased with each increasing N level ($P < 0.001$). Because there was little increase in growth above level N2, it appeared that both species were exhibiting some luxury consumption of N. Luxury consumption is defined here as uptake of a nutrient in excess of metabolic requirement. There were no significant differences in N concentrations as affected by P levels (Figs. III.3 and III.4).

Significant differences existed in N content over levels of N for both G. rossii and D. cespitosa ($P < 0.001$; Figs. III.3 and III.4). No differences in N content existed for G. rossii over P levels 2, 3, and 4 (Fig. III.3). Had P1 been included in the comparison, N content at this level probably would have been significantly lower than at the other levels. This is evident from the smaller shoot weights obtained at level P1 (see Fig. III.1 and Table III.1). N content varied among levels of P for D. cespitosa ($P < 0.001$; Fig. III.4).

P uptake in D. cespitosa was markedly different from N uptake. P concentration varied among levels of both P and N ($P < 0.001$; Fig. III.4). Level N1 plants had significantly greater P concentrations than did level N2, N3 or N4 plants. Although P concentrations at level P1 were significantly less than at all other levels of P, there were no significant differences in levels P2 and P3 or P3 and P4. These data

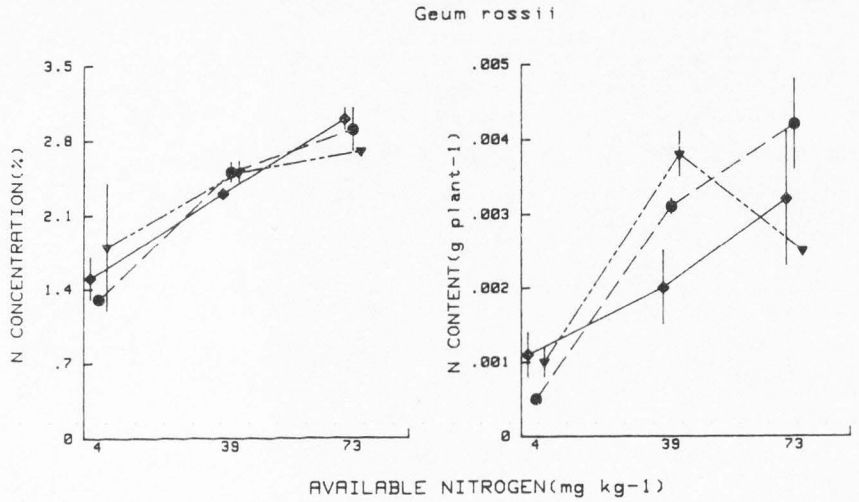

FIG. III.3. Mean N concentration and content of shoots of G. rossii seedlings harvested after 8 weeks growth in a factorial experiment at four levels of N and P as in Fig. 1.

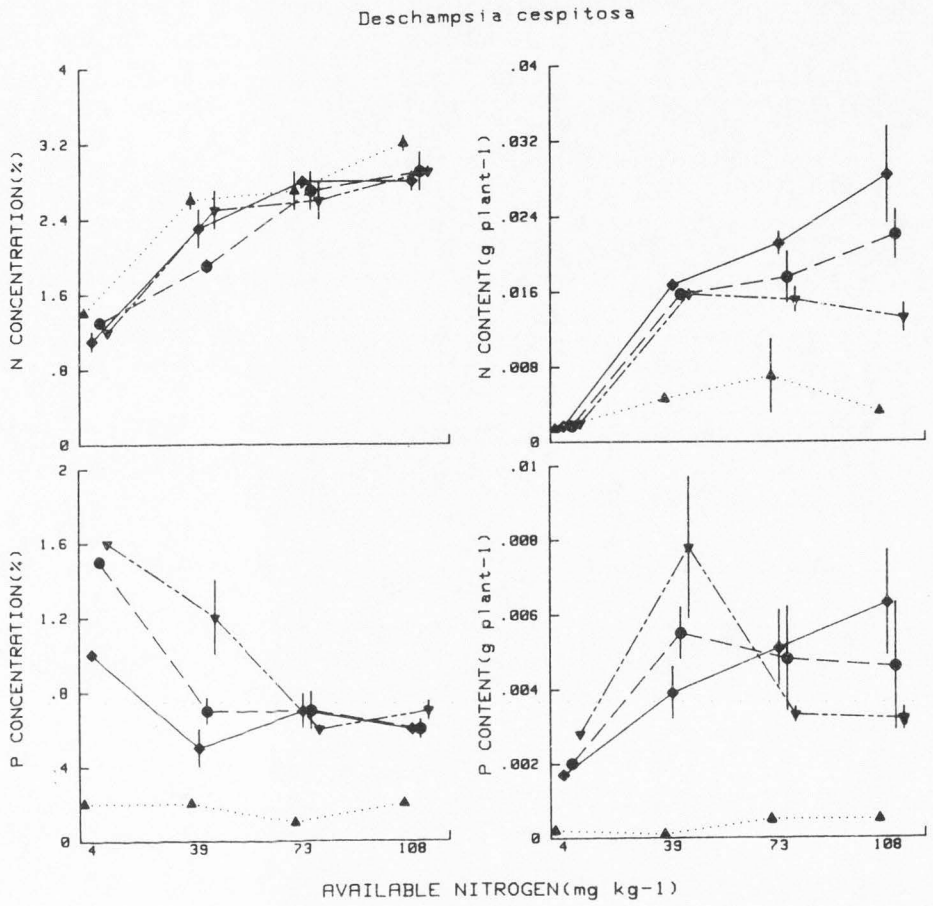

FIG. III.4. Mean N and P concentrations and contents of shoots of D. cespitosa seedlings harvested after 8 weeks growth in a factorial experiment at four levels of N and P as in Fig. 1.

indicate that above some minimum level of N, D. cespitosa can largely regulate its uptake of P.

P content of D. cespitosa differed only among levels of P ($P < 0.01$). Level P1 resulted in significantly lower P contents than all other levels of P ($P < 0.05$). This difference was observed because the response of shoot weight to P level was essentially the same as that of P concentration.

DISCUSSION

Experimental limitations

Use of native soils and growth under glasshouse conditions require caution in interpreting the results of nutrition studies. The native alpine soil had a total N content of 80.0 mg/kg and due to glasshouse conditions, N mineralization in excess of field conditions may have occurred. Also, the high sand content of the soil (63.4%) and recycling of leachate may have contributed to unnaturally high nutrient availability in treatments with added nutrients. In alpine ecosystems, fluxes in nutrients, especially N, occur during the growing season (e.g., Haselwandter et al. 1983), and may be more important than total pool sizes. Fertilizer additions can result in soil pH changes and consequently, differences in nutrient availability between treatments. In addition, relatively high growing temperatures and optimal soil water conditions experienced in glasshouses can result in higher rates of growth and nutrient uptake than in native alpine systems.

Maximum growth response of G. rossii and D. cespitosa was obtained at levels of N and P that were lower than those recommended for most crop species (Tisdale and Nelson 1975), but higher than those suggested for revegetating with native species in the western United States (Tiedemann and Lopez 1982). Because only N and P were added to the alpine soil instead of a complete nutrient formula, other mineral nutrients may have been limiting. However, the continued increase in growth response for certain N/P combinations above N2P2, and the lack of visual symptoms of other deficiencies, indicates that other nutrients were not controlling the growth response.

Successional implications

Differences between the two species in growth responses, response to N, and P and N uptake were consistent with the responses of species from temperate regions to changing nutrient levels during succession. The late seral dominant forb, G. rossii, responded more like a species from a low-nutrient environment than the early seral dominant grass. Species characteristic of low-nutrient environments often have higher (Davidson 1969) and less changing R:S ratios (Fitter and Hay 1981) and lower RGRs (e.g., Clarkson 1967, Chapin 1980). The high R:S ratios and low RGRs of G. rossii are typical of species with a capacity to tolerate low nutrient levels.

Plants from low-nutrient environments frequently exhibit luxury consumption of the limiting nutrients to take advantage of nutrient pulses (Chapin 1980). Alpine soils are characterized by generally low nutrient availability (Retzer 1974) and nutrient pulses (Haselwandter et

al. 1983). The apparent luxury consumption of N by G. rossii and D. cespitosa indicates adaptations to these conditions. The growth differences between the species may be explained by a more efficient use of N by D. cespitosa (higher RGR, a wider range of adaptability to N, or both).

In a study of the seasonal variation of N and P concentration in D. cespitosa growing on three different native soils, leaf N concentration varied over sites and seasons from approximately 0.9% to 2.4% (Davy and Taylor 1975). These concentrations are similar to the range exhibited in this study for all but the highest level of N. In contrast, leaf P concentration varied from approximately 0.07% to 0.18% (Davy and Taylor 1975). These concentrations correspond only to the lowest level of P in this study. This may indicate luxury consumption of P above level P1 in this study, or inherently low levels of P in the soils examined by Davy and Taylor (1975).

Evidence exists that early seral species from low-nutrient environments can exhibit growth and nutrient absorption characteristics similar to early seral species from high nutrient environments, that is, large RGRs and high nutrient absorption efficiencies (Tilman 1986). Early successional species from a prairie ecosystem with lower levels of N in early seres than in later seres, had higher RGRs and acquired more N per plant at both low and high N levels than did late successional species (Tilman 1986). It was suggested that the growth and nutrient absorption characteristics of these early seral species make them superior competitors for N and allow them to dominate in early succession. Early seral species were believed to be replaced by later

seral species during succession because other factors, such as light, become more limiting than nutrients (Tilman 1985, 1986).

An examination of N and P levels in soils from early and late successional alpine sites in the Beartooth Mountains showed that late seres had 5 to 10 times more P than paired early seres, but only 1.5 times available N (NO_3^- plus NH_4^+) (Chambers et al. 1987a). D. cespitosa exhibited greater rates of growth than G. rossii at all levels of both N and P. The greater growth response of D. cespitosa to levels of N and P indicates competitive superiority over a wide range of N and P concentrations. However, the higher sensitivity of G. rossii in terms of RGR and R:S ratio to levels of P, underscores the importance of P late in succession in this ecosystem. Soil P levels could affect competitive outcomes between these two species in early seral stages. This study indicates that competition studies between early and late successional species based upon single nutrients have serious limitations, and that field studies are needed to verify the results.

Revegetation recommendations

In this study, D. cespitosa and G. rossii were selected to bracket the range of life forms and successional affinities in the Geum turf community. The large differences in growth responses and nutrient uptake characteristics were predictable based upon the early and late successional categorization of the two species. Therefore, we feel that the responses of these species can be used to recommend N and P fertilizer rates and ratios for establishing similar early and late seral dominants in alpine revegetation efforts. Addition of N and P to

native alpine soil in this study increased the growth rate of D. cespitosa, the early successional grass, and G. rossii, the late successional forb, by 20% to 30%. Increased growth rates are a key factor for plant establishment on revegetated alpine disturbances (e.g., Brown et al. 1978). The maximum growth responses of D. cespitosa and G. rossii occurred at levels of both N and P in the soil between 40 and 70 mg/kg. These levels are higher than those commonly used in western mined land reclamation (Tiedemann and Lopez 1982) and should be interpreted with caution. Plants grown under glasshouse conditions may not respond like plants grown under field conditions and field trials are needed to verify these results. In this study, G. rossii exhibited toxicity at the highest level of N over all levels of P; the highest level of P had an adverse affect on D. cespitosa. This indicates that for mixed species plantings, the ratio of N to P should be close to 1:1.

High RGRs may provide competitive advantage for early successional species whatever the soil nutrient status, e.g., Tilman (1986). In a study of the competitive interactions of three perennial grasses under N stress, the effect of competition on yield decreased relative to unstressed plants, but the competitive outcome was not changed (Mahmoud and Grime 1976). High rates of fertilization or repeated fertilization can enhance the competitive ability of early successional species with high RGRs (e.g., DePuit and Coenenberg 1979). Proportionately larger increases in RGRs in response to fertilization permit these species to more effectively utilize available resources. To promote establishment of late successional species with low RGRs in mixed communities, it is necessary to decrease seeding densities of all species or to increase the relative seeding density of species with low RGRs.

The effect of low growth rates on survival may only be detectable when nutrient availability is low (Clarkson 1967). Including late successional species that are adapted to low-nutrient conditions and that have low RGRs can ensure the stable long-term productivity of nonintensively managed reclaimed areas. Use of late seral species can also increase the rate of succession.

CHAPTER IV

SEVERE VS. GAP-TYPE DISTURBANCE: EFFECTS OF SEEDLING ENVIRONMENT ON EMERGENCE, GROWTH, AND SURVIVAL OF EARLY AND LATE SERAL DOMINANT ALPINE PLANTS

INTRODUCTION

The intensity of disturbance is an important determinate of the properties of the seedling environment, and consequently, the species that establish following any given disturbance (Grubb 1977, White 1979, Bazzaz 1983). In alpine ecosystems two types of disturbances can be distinguished. (1) Small gap-type disturbances, those that leave surface soil horizons in place, result from cryogenic soil movement, e.g., solifluction and frost-heave (Johnson and Billings 1962), or biotic factors, e.g., small mammal tunneling and burrowing (Thorn 1982). (2) Severe disturbances, those in which soil surface horizons are removed, are caused by geomorphological processes such as landslides and avalanches. When surface horizons remain in place the predicted outcome is a short-term increase in nutrient availability above that of undisturbed areas because of decreased plant uptake and increased mineralization rates (Vitousek 1985, Vitousek et al. 1979). Following severe disturbance, soils are frequently less well-developed and nutrient availability is lower than on either gap-type disturbances or undisturbed areas (Chapin 1983). On both types of disturbances removal of vegetation can result in increased soil water

potentials because of decreased plant uptake of available water, and higher soil temperatures because of a lack of insulating vegetation (Vitousek 1985).

Grime (1977, 1979) categorized species according to their response to the effects of disturbance and the resulting productivity of the environment. Species typical of severely disturbed but potentially productive environments were termed ruderals, while species of productive, relatively undisturbed environments were called competitives. Ruderal species were characterized as lacking in competitive ability, being good colonizers with large reproductive potential, having high initial growth rates, and being short-lived. Competitive species were described as being finely tuned to their environment, highly competitive, reproducing at low rates, slow growing, and long-lived. Stress-tolerant species were those from continuously unproductive environments that had evolved special adaptations to the environmental contitions. Using this terminology, in relatively productive environments ruderals would dominate in early seres and competitives would dominate in late seres. In nonproductive environments stress tolerant species would dominate at all stages.

Successional processes on disturbed areas in alpine ecosystems are less apparent than those in more temperate systems (MacMahon 1980). Only a limited pool of species adapted to the extreme environment exists, and colonization following a disturbance is necessarily dependent upon members of that pool (Muller 1952). Succession in alpine ecosystems follows directional changes leading to the steady state or climax (Churchill and Hanson 1958, Bliss 1962), and distinct differences in species composition can be observed

between early and late seral stages (Webber and Ives 1978). Early seral disturbed sites in the Beartooth Mountains, Montana, contain alpine species that occur consistently and in higher abundances than other species on numerous types of alpine disturbances (Chambers et al. 1984). Similar observations have been made in the White Mountains, New Hampshire, USA (Roach and Marchand 1984). We define three successional categories. Late seral dominants are long-lived species that are most often found in late seral ecosystems, but that also colonize disturbed sites with suitable edaphic and topographic characteristics. These species fit within Grime's (1977, 1979) competitive classification. Moderately long-lived species that are frequent early colonizers, that exhibit wide geographic distributions and large ecological amplitudes, and that are rare on late seral areas are early seral dominants. These species are intermediate between Grime's (1977, 1979) competitive and ruderal classifications. A third category corresonds to Grime's (1977, 1979) ruderal species. Short-lived, rapidly growing species that occur almost exclusively on disturbed sites are early seral ruderals.

Although few studies have examined the mechanisms of alpine plant regeneration, it has been generalized that sexual reproduction is less important than vegetative propagation (e.g., Billings and Mooney 1968, Bliss 1971, Grime 1979). However, seed studies of species from various alpine environments indicate that many species produce viable seed (Bliss 1958, Amen and Bonde 1964, Bonde 1965, Amen 1966, Sayers and Ward 1966, Marchand and Roach 1980, Reynolds 1984, Haggas et al. 1987, Chambers et al. 1987c) and that seed dormancy occurs in only 20-40% of the species (Bliss 1985). In addition, successful seedling

establishment of alpine species has been observed under natural conditions (Brink 1964, Bonde 1968, Osburn 1961, Bliss 1971, Jolls and Bock 1983) and following seeding or transplanting experiments (Harrington 1946, Brown et al. 1976, 1978, Selner and King 1977, Roach and Marchand 1984). Recent studies indicate that for tundra ecosystems, seedling recruitment may be the most common means of colonizing disturbances (Freedman et al. 1982, Gartner et al. 1983).

Few quantitative data exist on the effects of disturbance type on seedling environment, or on the effects of differences in seedling environment on emergence, growth, or survival of different species. Previous studies in alpine ecosystems indicate that seedling establishment is dependent upon proper growing conditions and is frequently episodic (Bliss 1985). High seedling mortality has been attributed to needle ice activity (Osburn 1961, Brink et al. 1967, Bliss 1971, Roach and Marchand 1984), soil drought (Bonde 1968, Bliss 1971, Bell and Bliss 1980), or slow seedling development (Wager 1938, Bell and Bliss 1980).

Seedling establishment in tundra ecosystems occurs on organic turf soils and mineral soils, and is usually greatest in moist microhabitats (Bonde 1968, Bliss 1971, Jolls and Bock 1983) and in the absence of competition (Bonde 1968, Gartner et al. 1983). Organic mulches benefit seedling establishment by decreasing soil water loss and increasing soil surface temperatures. In addition, mulches can prevent surface wind erosion of both soil and seeds and, in some instances, may trap wind-blown seeds and soil. Neeedle ice is less likely to form in areas protected by vegetation and surface organic layers (Brink 1964). Seedling survival in arctic tundra was

restricted to moss or lichen mats and desiccation cracks (Bell and Bliss 1980).

Levels of soil nutrients may affect seedling growth and survival. Primary production of tundra ecosystems is frequently nutrient limited, due to cold soils and slow rates of decomposition. (Chapin 1981, Shaver and Chapin 1986). On severely disturbed alpine mine soils nutrient amendments increased seedling establishment (Brown et al. 1976, 1978). In contrast, on disturbed tundra sites with surface soil horizons in place, fertilization had no effect on survival (Roach and Marchand 1984), or increased mortality because of greater competition (Gartner et al. 1983).

Certain factors, including soil water, temperature, and nutrients and weather variables appear to be primary determinants of seedling establishment in alpine ecosystems. It is predicted that these factors differ between severe and gap-type disturbances, that individual species reponses to these factors vary, and that species reponses are related to their successional affinity. This study compares the soil environment and seedling emergence, growth, and survival of early and late seral dominants on an undeveloped alpine soil typical of a severe disturbance, with those on a highly organic, well-developed soil representative of a gap-type disturbance. In addition to evaluating differences between the two types of areas, specific comparisons were made within each disturbance type. The severely disturbed area was used to examine the effects of nutrient addition and mulching on the soil environment and on seedling emergence, growth, and survival. The undisturbed area was used to determine if differential establishment of early and late seral

dominants would occur between native, uncleared turf and native turf cleared of vegetation.

Some of the factors that affect seedling establishment in alpine ecosystems are addressed with three related questions: (1) What are the relative roles of soil water potential, soil temperature, and soil nutrients in emergence, growth, and survival of seedlings in a disturbed alpine ecosystem and how are these affected by disturbance type? (2) Are differences in emergence, growth, and survival of early and late seral dominants related to disturbance type? (3) What effect do soil treatments, viz., mulch and fertilizer, have on soil water potential, soil temperature, and soil nutrient relations in a disturbed alpine ecosystem, and consequently on seedling emergence, growth, and survival? (4) How do seedling emergence and survival on a native, undisturbed area differ from those on a gap-type disturbance within the same area?

STUDY AREA

The study was conducted on the Beartooth Plateau in south-central Montana, USA ($45^{o}00'$ N, $109^{o}30'$ W, elevation 3200 m), within the Geum turf vegetation type (Johnson and Billings 1962). Two kinds of sites were selected for plot installation: (1) a disturbed area from which all topsoil had been removed, and (2) an adjacent undisturbed area. The disturbed area was part of a 30-year old gravel barrow pit that had loamy sand soils and that had been sparsely colonized by plants (< 15% vegetation cover). The undisturbed area, located approximately 150 m from the disturbed area, had turf soils

and vegetation cover greater than 90%. Both areas were east-facing and situated on slopes of less than 5%.

Weather of the area was monitored from 30 June to 14 September in 1985 and from 25 June to 6 September in 1986. All instrumentation was placed at or near ground level to accurately sample the seedling environment. The values obtained were similar to those from other North American alpine areas (see Bliss 1985). Mean wind velocity, measured with a totalizing anemometer positioned 40 cm above the ground, was 36.7 m/s in 1985 and 40.0 m/s in 1986. Photon flux densities were determined with a Li-Cor solar monitor (LI-1776) that recorded wavelengths between 400 to 700 nm. Levels measured were high; the daily midday average (1200-1300 hr) was 1723 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in 1985, and 1501 $\mu mol \cdot m^{-2} \cdot s^{-1}$ in 1986. Maximum recorded solar radiation was 2225 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at 1400 h on 25 July 1985 and 2267 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at 1300 h on 26 June 1986. Precipitation was obtained at two-week intervals. The cumulative value recorded for 1985 was 102 mm and that for 1986 was 152 mm (Table IV.1). Temperature was determined from a 31-day recording WEATHERtronics hygrothermograph (model 5022) placed at ground level within an instrument shelter. Mean maximum and minimum daily temperatures differed during the two years, 14.7°C and 2.9°C, respectively, in 1985, and 13.7°C and 1.0°C in 1986 (Fig. IV.1).

TABLE IV.1. Growing season precipitation on the Beartooth Plateau during 1985 and 1986.

1985		1986	
Time Interval	mm	Time Interval	mm
30 June - 7 July	1.8	25 June - 31 June	7.9
7 July - 23 July	22.8	31 June - 17 July	27.4
23 July - 31 July	48.3	17 July - 22 July	15.5
31 July - 16 Aug	0.0	22 July - 11 Aug	27.4
16 Aug - 22 Aug	1.8	11 Aug - 16 Aug	29.0
22 Aug - 10 Sept	26.9	16 Aug - 6 Sept	45.2
TOTAL	101.6	TOTAL	152.4

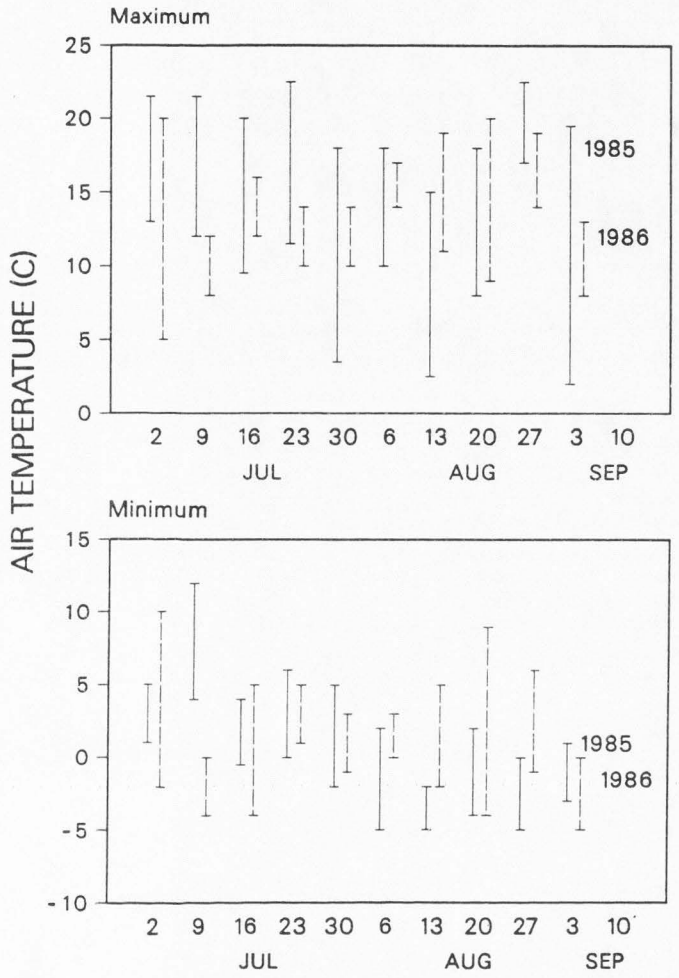

FIG. IV.1. Ranges in maximum and minimum air temperature for one week periods during 1985 and 1986 on the Beartooth Plateau, Montana.

METHODS

Experimental design

On the disturbed area, the study design included seeded plots with two levels of fertilization and mulch ("optimal" and none) and unseeded control plots (2x2+1). On the undisturbed area, the design included plots cleared of native vegetation or not-cleared of native vegetation and seeded or not-seeded (2x2). Seeded main plots on both areas were subdivided into 6 subplots, each containing one of three early or late seral dominant species. A randomized block design with 3 replications of each treatment was used on both areas (Fig. IV.2). Treatment main plots were 3 m by 1.5 m and species subplots, randomized within main plots, were 1.5 m by 0.5 m. One half of each subplot was used for destructive sampling, while the other half was reserved for nondestructive sampling (Fig. IV.3).

Soil samples were collected from each of the main treatment plots on both areas 19 August 1984. One sample, consisting of a 7.5 cm x 10 cm core, was collected from each plot. Samples were analyzed by A & L Labs, Omaha, Nebraska, for organic matter, total N, NO_3, NH_4, P, K, cation exchange capacity (CEC), pH, and texture using the methods described in Chambers et al. (1987a). To evaluate change in soil nutrient status during the 2-year duration of the study, soil samples were again collected from the plots in an identical manner on 15 August 1986 and the same analyses were performed.

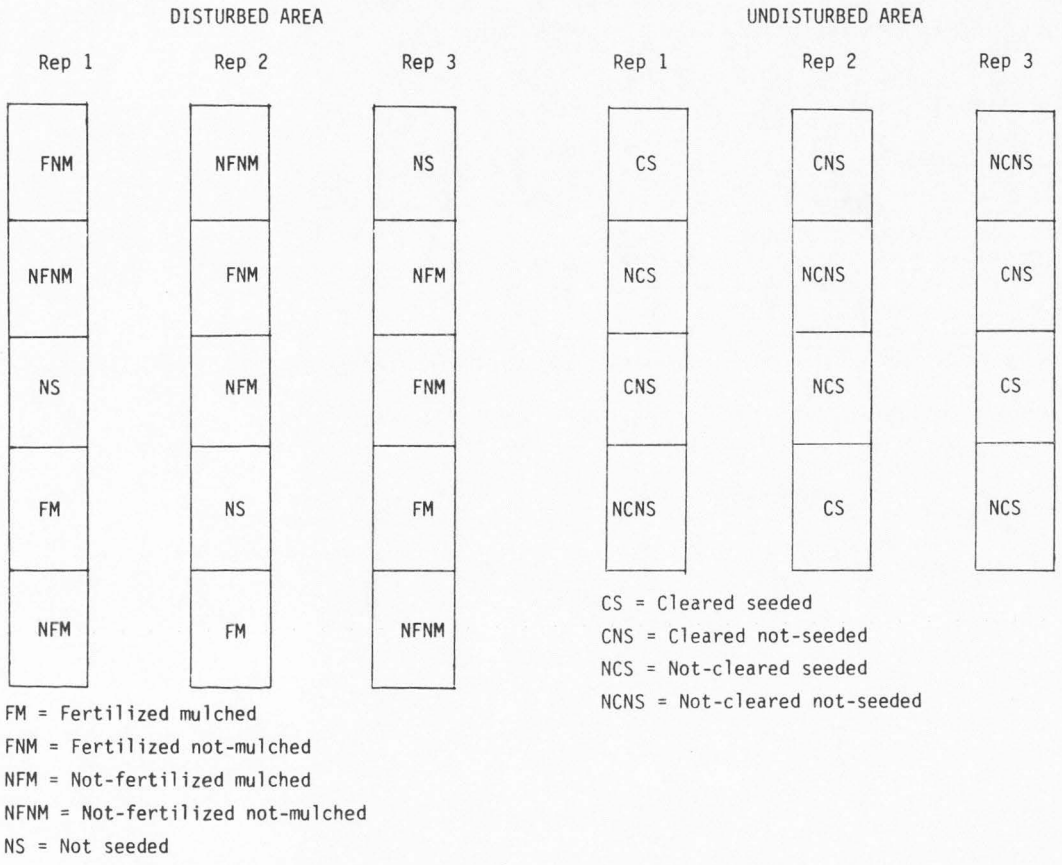

FIG. IV.2. Randomized block study designs for the disturbed and undisturbed areas on the Beartooth Plateau, Montana.

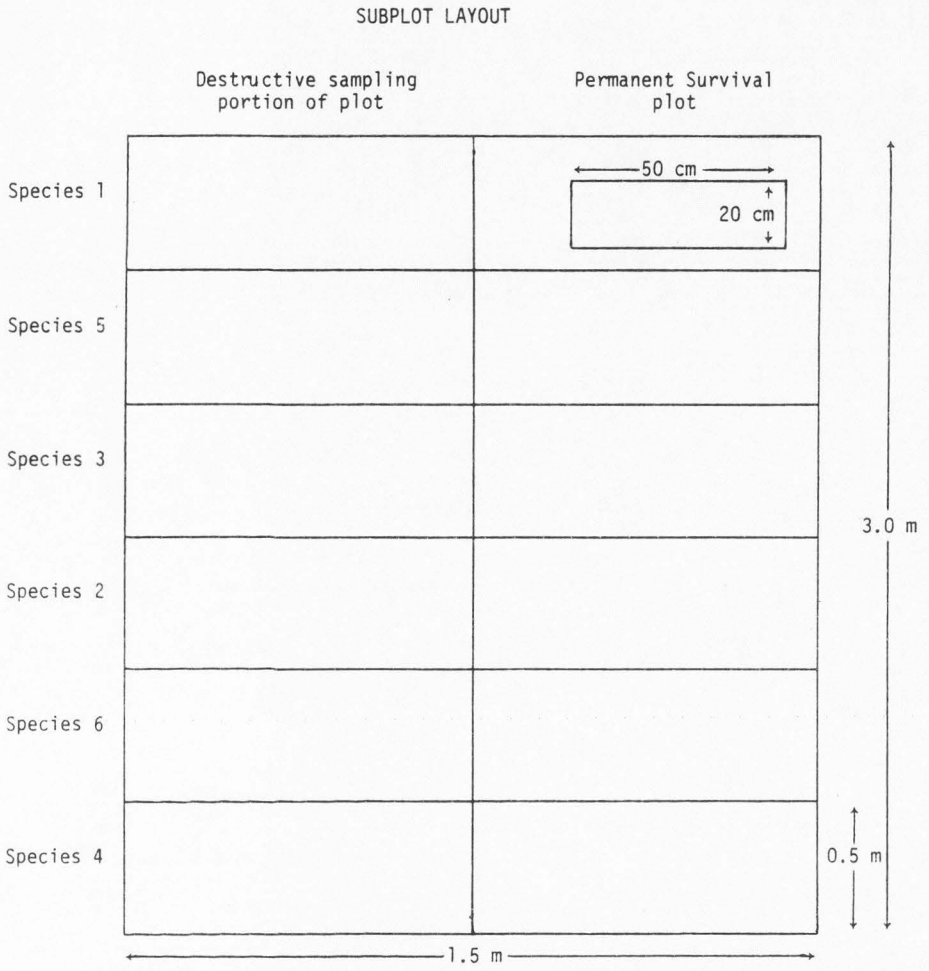

FIG. IV.3. Subplot layout for randomized block designs used on the disturbed and undisturbed areas on the Beartooth Plateau, Montana.

The "optimal" level of fertilization on the disturbed area was determined from a preliminary greenhouse experiment that examined the effects of 4 levels of N in combination with 4 levels of P on the growth and nutrient uptake of Deschampsia cespitosa, an early seral dominant, and Geum rossii, a late seral dominant (Chapter III). The amounts of N and P used in the field were 8.2 g/m and 15.6 g/m, respectively, applied as $(NH_4)_2HPO_4$ and $CaH_4(PO_4)_2$. The type and level of mulch was selected based upon the results of studies that have examined seedling establishment under different mulching regimes (e.g., Meyer et al. 1971, Kay 1983). In this study, 224 g/m of straw mulch were applied.

The species studied are broadly distributed throughout the central and southern Rocky Mountains and occur naturally within the Geum turf community on both late seral (Johnson and Billings 1962) and early seral sites (Chambers et al. 1984). The successional classification of early or late seral dominant was derived from cluster analyses of species found on disturbed alpine sites in the Beartooth Mountains, Montana (Chambers et al. 1984) and on descriptions of late seral alpine communities in the same area (Johnson and Billings 1962). Seeded species included two late seral dominant forbs, Geum rossii (R. Br.) Ser., and Artemisia scopulorum Gray,; two early seral dominant forbs, Sibbaldia procumbens L. and Potentilla diversifolia Lehm.; one late seral dominant grass, Festuca idahoensis Elmer; and one early seral dominant grasses, Deschampsia cespitosa (L.) Beav. In addition, survival of 5 early seral ruderal species that occurred as unseeded colonizers on the plots was monitored. These included: Draba crassifolia R. Grah., Draba incerta

Pays., Cerastium arvense L., Arenaria obtusiloba (Rydb.) Fern., and Androsace septentrionalis L.

Seeds were collected adjacent to the study areas in September 1983. Seeds of late seral dominants were collected from undisturbed areas and seeds of early seral dominants were gathered from disturbed early seral areas. After harvest, seeds were allowed to dry for 2 weeks, threshed, fanned to remove light and unfilled seed, and stored dry at 1-2^{o}C until use. Seeding rates and methods were determined from a separate experiment that examined the effects of light and stratification (cold wet storage) on seed germination of the different species (Chapter II). Germination percentages of seeds that received wet cold storage and that were germinated in the dark were used to determine field seeding rates. This treatment approximated field conditions. The quantities of seeds actually used were derived on the basis of dry weight equivalents. Seeding densities were calculated to produce an average spacing of 5 cm between individual seedlings, a distance believed to minimize competitive interactions.

Plots on both areas were seeded on 10 September 1984. On the disturbed area, N and P were applied to treated main plots prior to seeding by first mixing fertilizer pre-weighed for each plot with 6 L of soil obtained adjacent to the study plots, and then sprinkling the mixture uniformly over main plots. Seed was then applied to all seeded main plots on an individual subplot basis. On all seeded plots on the disturbed area and on the cleared and seeded plots on the undisturbed area, seed for each subplot was mixed with 2 L of soil collected adjacent to the study plots and sown over the subplot. On the undisturbed area seeded, not-cleared treatment, seed alone was

sown onto the subplots. Mulch was applied to specified main plots on the disturbed area after the subplots were seeded. To insure that the mulch would not be blown away, it was "sandwiched" between 2 layers of plastic Conwed (1.3 cm) netting and staked firmly in place with U-pins.

Seedling establishment on the undisturbed plot was extremely poor in 1985 and the seeded treatment was reapplied 10 September 1985. The same procedures as were originally used were repeated on the seeded, not-cleared plots. On the cleared plots seed was mixed with 6 L of soil and after seeding plots were covered with 2 layers of Conwed netting. The same seed lot was used but new seeding rates were calculated that incorporated 1985 viability percentages determined using methods in Chapter II.

Plot sampling was conducted during 4, 7-10 day periods in both 1985 and 1986 growing seasons. Intervals between sampling periods were approximately 2-weeks.

Soil water potential was measured twice during the first 3 sampling periods and once during the last period of both years with screen-caged single junction Peltier thermocouple psychrometers (JRD Merrill Series 84). One sample was taken from each main plot on both areas at depths of 5 and 15 cm from the portion of the plot reserved for destructive sampling. Samples were extracted from the appropriate depth with a small soil corer and sealed in a stainless steel calibration chamber (3.5 cm^3). Water potential values were obtained using the methods of Brown and Bartos (1982).

Soil temperature was measured during the study with copper-constantan thermocouples installed prior to plot seeding.

Within each main plot a network of 3 interconnected thermocouples of equal length, spaced 50 cm apart, were buried at depths of 5 and 15 cm. Using three connected thermocouples provided an integrated temperature for each depth and having leads of equal length insured uniform average voltage output. Surface temperatures were determined from a 10 cm x 10 cm perforated copper plate that was installed 2-3 mm beneath the surface. Soil temperatures were obtained at 1200 hr daily during each of the sampling periods with a Decagon nanovoltmeter (model NT-3).

Seedling survival was recorded within each subplot and control during each sampling period. A mapping table and acetate overlays were used to census seedlings within the plots and to relocate mapping areas (Appendix A). Mapping areas were permanently marked with steel stakes. Precise relocation of mapping areas and seedlings was achieved by using an alignment device. Introductions and deaths of both seeded and colonizer species were recorded. Seedlings that had emerged since the previous census were placed in the same cohort.

Seedlings of all 6 seeded species were harvested from the portion of the subplots reserved for destructive sampling on 17 August 1985 and 15 August 1986. An attempt was made to collect 10 individuals from every subplot, but this was not possible for all treatments or species. To minimize bias in selecting harvested individuals, seedlings were harvested at 5 cm intervals along transects placed 10 cm from the upper plot boundary in 1985 and 10 cm from the lower plot boundary in 1986. Roots were carefully washed and separated from shoots. Plants were oven dried at $70^{\circ}C$ for 24 h.

Data analysis

Analysis of Variance (ANOVA) was used to examine differences among sites and treatments for soil temperature, soil water potential, and harvest data. The sources of variation and the degrees of freedom for the 2-year comparisons are shown in Appendix B. Separate ANOVAs were also performed on 1985 and 1986 data alone. Comparisons among sites of soil chemical properties, water potential, and temperature were performed with unseeded control plots and seeded plots that were not fertilized or mulched on the disturbed area and seeded or not-seeded plots that were cleared of vegetation on the undisturbed area. Because the treatments were not interspersed, differences among sites but not treatments were evaluated (see Hurlbert 1984). Analyses similar to those conducted on soil temperature and water potential data were performed on soil chemical property data, except that depth and period were not included as factors. Mean comparisons were evaluated with Fisher's Protected LSDs. Sampling periods were treated as repeated measures and incorporated into the ANOVA design as split-plots for the soil temperature and water potential data.

Seedling emergence and survival data were analyzed with categorical data analysis (CDA) (Fienberg 1985). CDA is appropriate for analyzing cross-classified categorical data such as the emergence 3nd survival data collected in this study. Multidimensional contingency tables are analyzed using loglinear models similar to ANOVA models to describe the structural relationships among the variables corresponding to the dimensions of the table. CDA models are used to determine effects of explanatory or independent variables,

but can be converted into logit models to predict log-odds quantities of response or dependent variables from linear combinations of effects due to explanatory variables. In this study effects of the explanatory variables on seedling emergence or number of introductions was evaluated with CDA models. Log-odds mortality ratios were calculated from logit models in which number of individuals dead vs. alive was the response variable. Differences among calculated log-odds for significant explanatory variables were determined from all possible chi-square comparisons of the appropriate count tables of alive/dead pairs.

RESULTS

Soil chemical properties

Soil samples were collected in 1984 before plot establishment on either the disturbed or undisturbed areas. The 1984 samples from the disturbed area were compared with samples obtained in 1986 from control plots on the disturbed area; those from the undisturbed area were compared with samples obtained in 1986 from plots on the undisturbed area that were neither cleared of vegetation nor seeded. Few statistical differences existed between years for any of the properties examined. Levels of NO_3 were significantly higher on the disturbed area in 1984 than in 1986. This probably resulted from removing all vegetation from the disturbed area in 1984 after collecting the soil samples, but before establishing the plots.

Analysis of 1986 data showed that for organic matter (OM), large differences existed between sites ($P < .001$) (Fig. IV.4). However, no differences were found among treatments within sites. Identical results were obtained for total nitrogen (TN). These findings indicate that surface mulching had no effect on OM or TN on the disturbed area. Also, clearing plots of vegetation did not alter OM or TN levels on the undisturbed area. NO_3 was significantly greater in fertilized than in not-fertilized plots on the disturbed area and in cleared than in not-cleared plots on the undisturbed area ($P < .001$). Levels of NO_3 on nonseeded vegetated plots on the undisturbed area were greater than nonseeded plots on the disturbed area that were not fertilized or mulched ($P < .001$). Amount of NH_4 was greater in fertilized plots than in nonfertilized plots on the disturbed area ($P < .001$), but no differences existed among treatments on the undisturbed area. The undisturbed area had significantly higher levels of NH_4 than the disturbed area ($P < .01$).

Levels of P were greater in fertilized than in not-fertilized plots on the disturbed area ($P < .001$), and in cleared than in not-cleared plots on the undisturbed area ($P < .001$) (Fig. IV.2). Also, P levels were higher on the undisturbed area than on the disturbed area ($P < .05$). Treatment had no effect on either K or CEC within sites, but both were significantly higher on the organic soils of the undisturbed area than on the sandy soils of the disturbed area ($P < .001$). pH was lower on fertilized than on not-fertilized plots on the disturbed area ($P < .01$), and on cleared than on not-cleared plots on the undisturbed area. In general, pH of the undisturbed site was less than that of the disturbed site ($P < .001$).

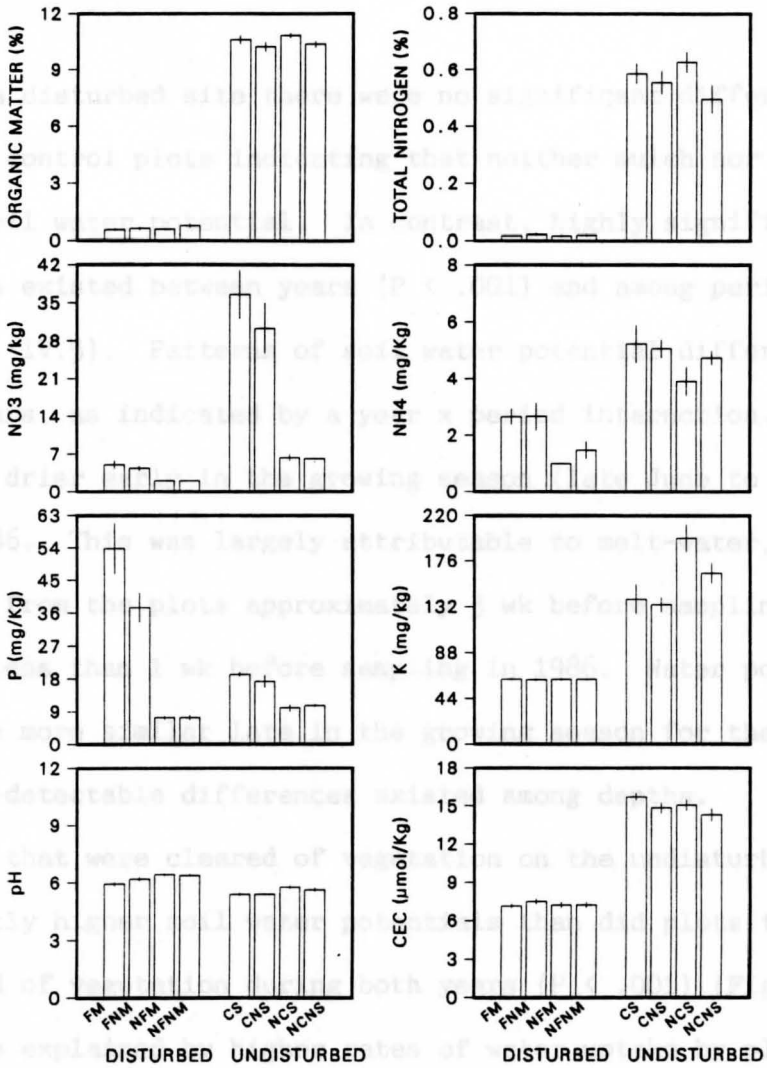

FIG. IV.4. Soil chemical properties of disturbed and undisturbed areas on the Beartooth Plateau, Montana in 1986. Treatment codes are: FM = fertilized, mulched; FNM = fertilized, not-mulched; NFM = not-fertilized, mulched; NFNM = not-fertilized, not-mulched; CS = cleared, seeded; CNS = cleared, not-seeded; NCS = not-cleared, seeded; NCNS = not-cleared, not-seeded. Values are means and error bars represent $\pm$ 1 SE; n = 6.

Soil water potential

On the disturbed site there were no significant differences among treated or control plots indicating that neither mulch nor fertilizer affected soil water potential. In contrast, highly significant differences existed between years ($P < .001$) and among periods ($P < .001$) (Fig. IV.5). Patterns of soil water potential differed between the two years, as indicated by a year x period interaction. In 1985, soils were drier early in the growing season (late June to mid-July) than in 1986. This was largely attributable to melt-water, as snow had melted from the plots approximately 3 wk before sampling began in 1985, but less than 1 wk before sampling in 1986. Water potential values were more similar late in the growing season for the two years. No detectable differences existed among depths.

Plots that were cleared of vegetation on the undisturbed site had significantly higher soil water potentials than did plots that were not cleared of vegetation during both years ($P < .001$) (Fig. IV.6). This can be explained by higher rates of water uptake by plants on plots with vegetation in place. On cleared plots, uptake by seedlings was insufficient to lower soil water potentials. Soil water potentials differed among years ($P < .05$) and periods ($P < .001$), but there were no differences among depths. A year x period interaction indicated that differences in patterns existed among the two years. This was particularly evident for cleared plots. Due to the early snow melt in 1985, the growing season began earlier than in 1986 and plant growth had largely ceased by mid-August. In 1986 plants were

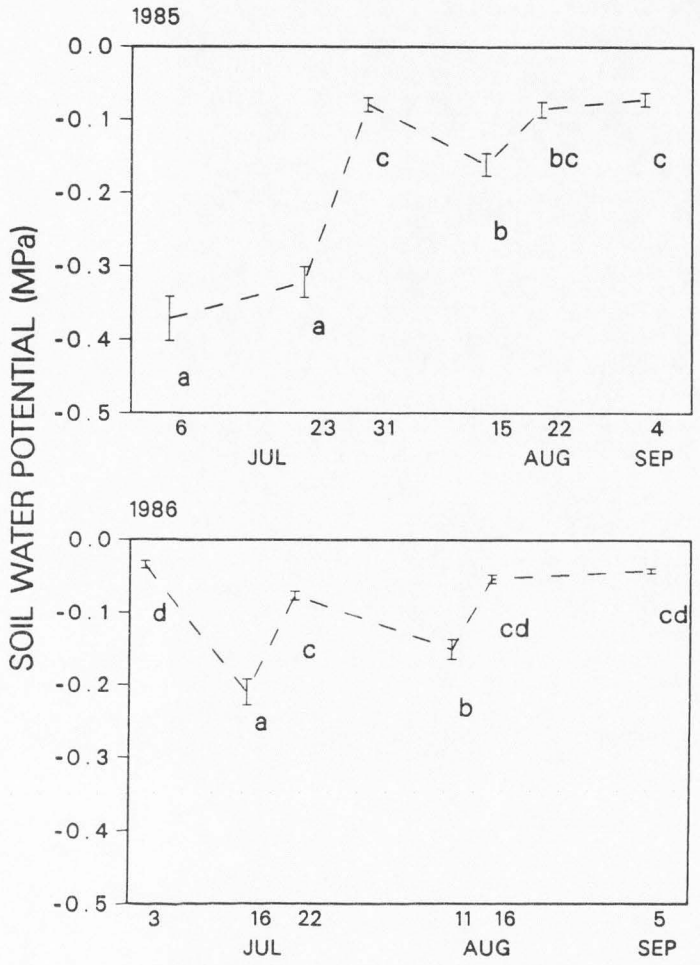

FIG. IV.5. Soil water potential values summed over treatments and depths for 1985 and 1986 growing seasons on the disturbed area, Beartooth Plateau, Montana. Values are means, error bars represent $\pm$ 1 SE; n = 45. Unlike letters indicate significant differences among periods ($P < .05$).

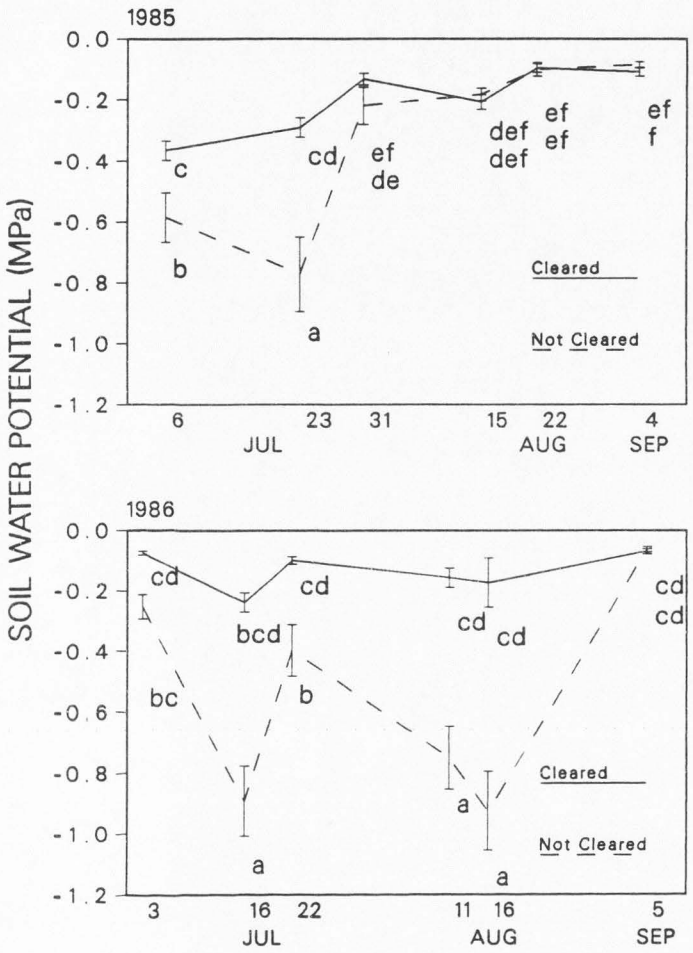

FIG. IV.6. Soil water potentials for cleared vs. not-cleared treatments summed over depths for 1985 and 1986 growing seasons on the undisturbed area, Beartooth Plateau, Montana. Values are means and error bars represent $\pm$ 1 SE; n = 18. Unlike letters indicate significant differences among treatments and periods ($P < .05$).

still actively growing in mid-August. A period x cleared plot interaction was found ($P < .01$), indicating that soil water potentials on cleared plots were not higher than those on not-cleared plots for all periods.

Significant differences existed among sites ($P < .01$). Patterns of soil water potential among years and over periods for the disturbed area were more similar to cleared plots on the undisturbed area than to plots not cleared of vegetation.

Soil temperature

Soil temperature data for cloudy vs. sunny days differed statistically for years, periods, treatments, and depths (ANOVA, $P < .05$). Therefore, cloudy and clear days were analyzed separately; 1 cloudy day for each of 4 sampling periods and 1 sunny day for each of 4 sampling periods. In addition, partially overcast days that resulted in highly variable soil surface temperatures within treatments were excluded from analysis.

On the disturbed area, few differences existed among treatments. Soil temperatures of mulched plots differed from those of unmulched plots on sunny, but not on cloudy days and only in 1985 ($P < .05$). A portion of the straw mulch was redistributed or removed from the plots by wind, and this decreased the insulating properties of the mulch over time. Highly significant differences among periods and depths existed on cloudy and sunny days during both years ($P < .001$) (Fig. IV.7). On clear days differences in temperatures among depths were much greater than on cloudy days. Differences were found among years

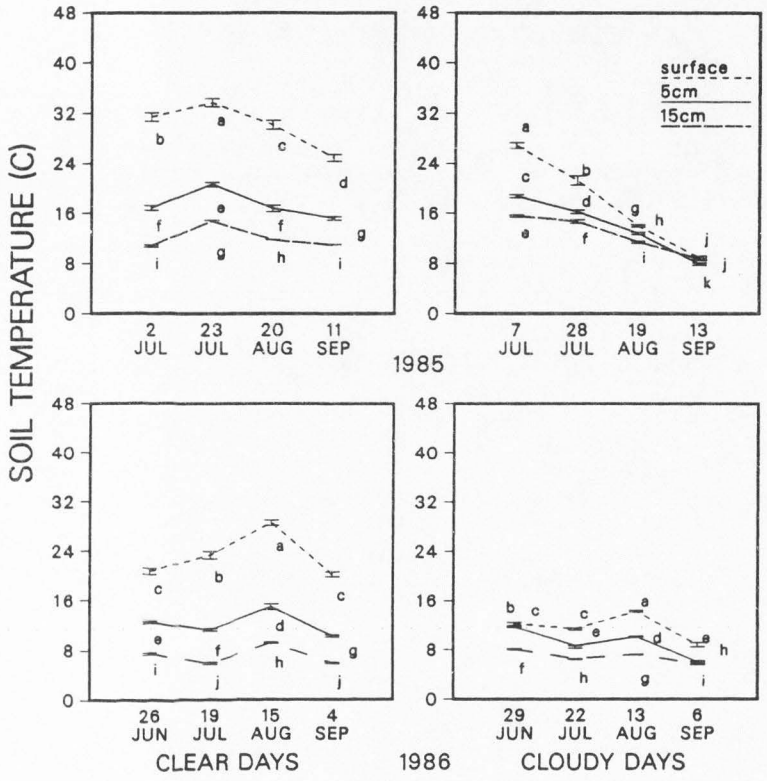

FIG. IV.7. Soil temperatures summed over treatments for surface, 5 cm, and 15 cm depths on clear and cloudy days during 1985 and 1986 growing seasons on the disturbed area, Beartooth Plateau, Montana. Values are means, error bars represent $\pm$ 1 SE; n = 15. Unlike letters indicate significant differences among depths and periods ($P < .05$).

($P < .001$) and a significant year x period interaction indicated that patterns of soil temperature varied among years ($P < .001$). In general, 1986 soil temperatures were colder early in the growing season than in 1985. Soil water potentials were lower during this time period (Fig. IV.5) as were ambient air temperatures (Fig. IV.1). A depth x period interaction was found on cloudy and sunny days for both years, because soil temperatures for a given depth were not consistently greater or less than those for the other two depths across periods.

Cleared plots on the undisturbed area differed from uncleared plots only in the two-year comparisons ($P < .05$). However, clearing x depth and clearing x period interactions were found ($P < .01$), indicating that the effects of clearing on soil temperature varied among periods and depths. Surface temperatures were similar for the two clearing treatments, but cleared plots had higher temperatures at both 5 and 15 cm depths (Fig. IV.8). The similarity in surface soil temperatures on cleared and not-cleared plots may have resulted from methods used to install the copper plates, and may not accurately reflect the surface temperatures on the vegetated plots. Vegetation was partially removed and plates were covered with organic soil and litter which may have decreased shading and increased heat conductance to the plates. There were statistical differences in depths on sunny and cloudy days for both years ($P < .001$). Year and period differences existed and there was a period x year interaction and period x depth interaction (all; $P < .001$).

Comparison of disturbed and undisturbed areas showed consistent differences among sites ($P < .05$). In general, soil temperatures

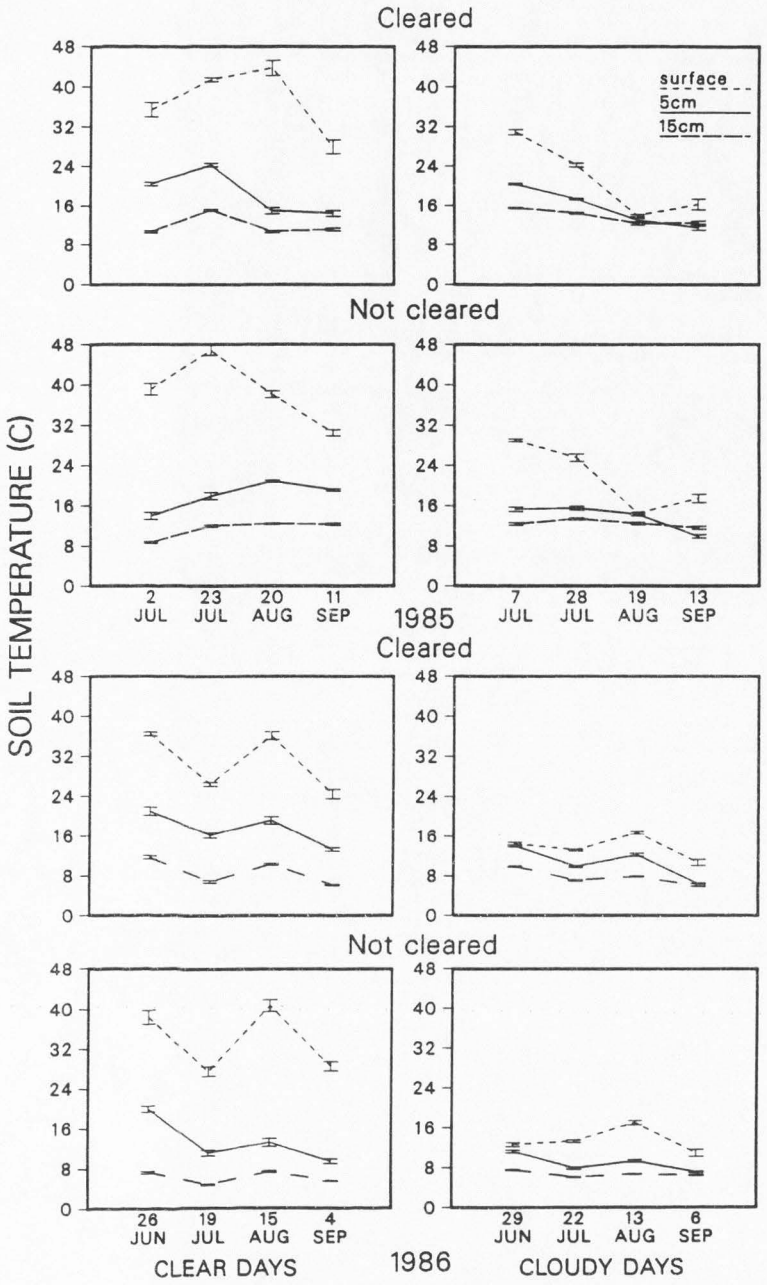

FIG. IV.8. Soil temperatures summed over seeding treatments for surface, 5 cm, and 15 cm depths on clear and cloudy days during 1985 and 1986 growing seasons on the undisturbed area, Beartooth Plateau, Montana. Values are means and error bars represent $\pm$ 1 SE; n = 12. Unlike letters indicate significant differences among depths and periods ($P < .05$).

especially at the surface, were higher on dark-colored, organic soils of the undisturbed area than on light-colored, sandy soils of the disturbed area.

Seedling growth

Harvest data analyses of disturbed area plots included separate analysis of individuals that emerged and were harvested in 1985, that emerged in 1985 but were harvested in 1986, and that emerged in 1986 and were harvested in 1986. Comparisons were also made of individuals harvested in 1985 on the disturbed area that established in 1985 vs. those that emerged and were harvested in 1986. Differences between disturbed and undisturbed areas were evaluated by comparing individuals that emerged in 1986. Seeded, cleared plots on the undisturbed area were compared with seeded plots on the disturbed area that either received no mulch and no fertilizer or that had been both mulched and fertilized. Separate analyses were performed for all species combined and for individual species. Due to small sample sizes and missing values on the disturbed area, F. idahoensis was excluded from all analyses and 1986 analyses were performed with P. diversifolia, D. cespitosa, and S. procumbens only.

Treatment comparisons of individual species on the disturbed area showed that regardless of successional affinity, seedling shoot and root weights of fertilized plots were greater than those of nonfertilized plots for all emergence-harvest dates (Table IV.2, Fig. IV.9). Exceptions included individuals of S. procumbens that had emerged in 1985 and were harvested either in 1985 or 1986 and

TABLE IV.2. Significance levels for shoot and root weights and R/R+S ratios from ANOVAs comparing treatment effects for individual species and all species combined on the disturbed area.

	Shoot Weight			Root Weight			R/R+S Ratio		
	Fertilizer	Mulch	Fertilizer x mulch	Fertilizer	Mulch	Fertilizer x mulch	Fertilizer	Mulch	Fertilizer x mulch
Emerged 1985 Harvested 1985									
Geum rossii	<.05	NS	NS	NS	NS	NS	<.05	NS	NS
Artemisia scopulorum	<.01	NS	NS	<.01	<.05	NS	NS	NS	NS
Potentilla diversifolia	<.01	NS	NS	<.05	NS	NS	NS	NS	NS
Sibbaldia procumbens	NS	NS	NS	NS	NS	NS	NS	NS	NS
Deschampsia cespitosa	<.01	<.05	NS	<.01	NS	NS	NS	NS	NS
ALL	<.05	NS	NS	<.01	NS	NS	NS	NS	NS
Emerged 1986 Harvested 1986									
Geum rossii	-	-	-	-	-	-	-	-	-
Artemisia scopulorum	NS	NS	NS	NS	NS	NS	NS	NS	NS
Potentilla diversifolia	NS	NS	NS	NS	NS	NS	NS	NS	NS
Sibbaldia procumbens	<.05	NS	NS	<.05	NS	NS	NS	NS	NS
Deschampsia cespitosa	<.05	NS	NS	<.05	NS	NS	NS	NS	NS
ALL	<.01	NS	NS	<.01	NS	NS	NS	NS	NS
Emerged 1985 Harvested 1986									
Geum rossii	<.05	NS	NS	<.05	NS	NS	NS	NS	NS
Artemisia scopulorum	<.01	<.05	NS	<.01	<.05	NS	NS	NS	NS
Potentilla diversifolia	<.05	NS	NS	<.05	NS	NS	NS	NS	NS
Sibbaldia procumbens	NS	NS	NS	NS	NS	NS	NS	NS	NS
Deschampsia cespitosa	<.05	NS	NS	<.01	NS	NS	NS	NS	NS
ALL	<.05	NS	NS	<.05	NS	NS	NS	NS	NS

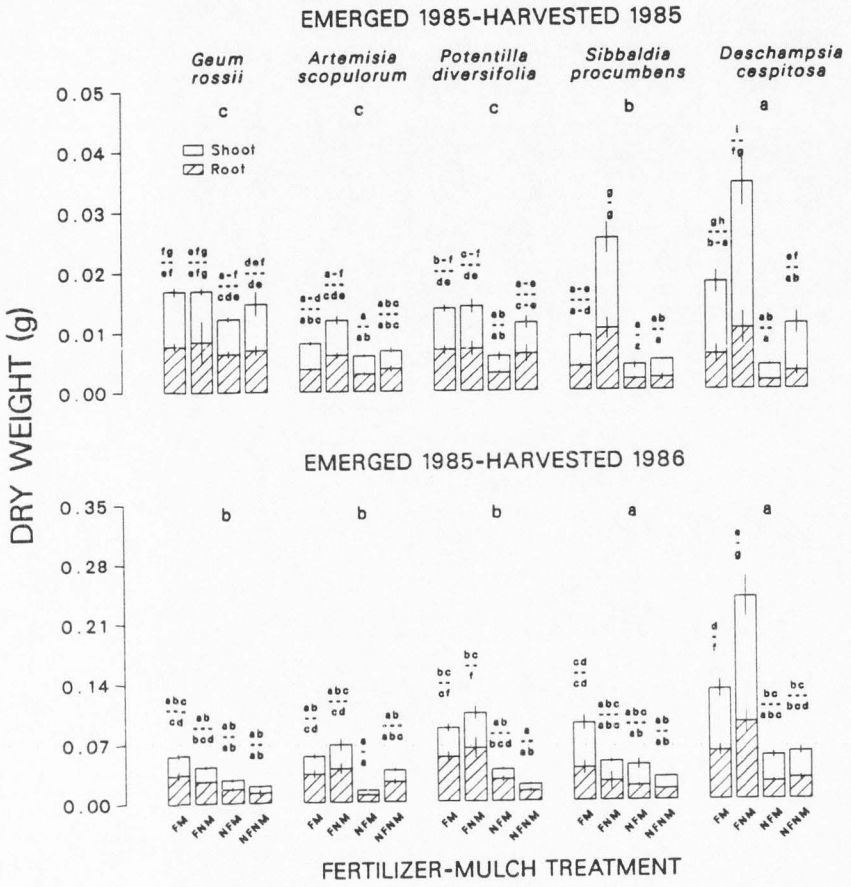

FIG. IV.9. Seedling root and shoot dry weights of individuals that emerged in 1985 and were harvested in 1985 or 1986 on the disturbed area, Beartooth Plateau, Montana. Values are means and error bars represent $\pm$ 1 SE; n is variable. Unlike letters indicate significant differences in R/R+S ratios among species, shoot weights among treatments and species, and root weights among treatments and species for the first, second, and third rows of letters, respectively ($P < .05$). Treatment codes as in Fig. 4.

individuals of A. scopulorum and P. diversifolia that had emerged and were harvested in 1986. In each of these cases, sample sizes were extremely small and lack of statisitical significance was probably a function of high sample variance. Fertilization had no effect on root to plant ratios (R/R+S), except for G. rossii which had higher ratios on nonfertilized than fertilized plots for individuals that emerged and were harvested in 1985 (Table IV.2). Harvesting intact root systems was extremely difficult in the field, and may have contributed to the lack of an observed response in R/R+S ratios.

Mulch affected seedling growth of only two species, A. scopulorum and D. cespitosa, and in both cases shoot or root weights were lower on mulched plots (Table IV.2). A. scopulorum had higher root and shoot weights for individuals that emerged and were harvested in 1985 and higher root weights for plants that emerged in 1985 and were harvested in 1986. As a result of increased effects of wind on nonmulched plots, this species in particular had large sections of root extending above the soil surface. This may have resulted in greater allocation to roots.

Differences among species in root and shoot weights and R/R+S ratios are shown in Figs. IV.9 and IV.10. Growth of early seral dominants exceeded that of late seral dominants, especially for certain species, treatments and harvest dates. Individuals of D. cespitosa that emerged and were harvested in 1985 and that emerged in 1985 and were harvested in 1986 on fertilized plots were significantly larger than those of most other species. By the end of the second growing season, individuals of S. procumbens and P. diversifolia were slightly larger than late seral dominants. First year seedlings of

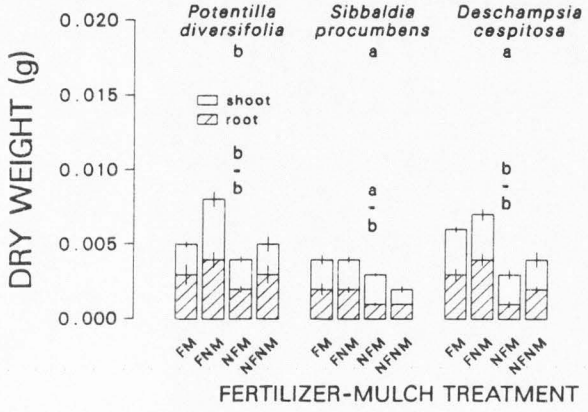

FIG. IV.10. Seedling root and shoot dry weight of individuals that emerged and were harvested in 1986 on the disturbed area, Beartooth Plateau, Montana. Values are means and error bars represent $\pm$ 1 SE; n is variable. Unlike letters indicate significant differences among species in R/R+S ratios, shoot weights, and root weights for the first, second, and third rows of letters, respectively ($P < .05$). Treatment codes as in Fig. 4.

late seral dominant, G. rossii, were consistently large across treatments, but this size difference did not persist through the second year. With few exceptions, R/R+S ratios were smaller for early seral dominants, S. procumbens and D. cespitosa, than for other species.

Comparison of first year growth of seedlings from the disturbed area harvested in 1986 showed that, in general, individuals from 1985 were larger than those from 1986 for all treatments ($P < .001$). The only exception to this trend was for root weights of S. procumbens and shoot weights of P. diversifolia and these exhibited no difference among dates. The larger individuals in 1985 may be explained by a longer growing season in 1985 than in 1986. Snow had melted from the plots earlier in 1985 and soil temperatures were warmer for a longer period of time (Fig. IV.1). Soil nutrient levels may also have been higher during the first year after ferilization than during the second.

Seedlings that emerged and were harvested in 1986 were larger on cleared plots on the undisturbed area than on either fertilized and mulched or not-fertilized, not-mulched plots on the disturbed area for the three species comparison ($P < .05$) (Fig. IV.11). This was especially striking for D. cespitosa.

Species comparison of seedlings that emerged and were harvested in 1986 on the undisturbed area showed no differences in either root or shoot weights among forbs. However, significant differences existed between grasses and forbs and among grasses (Fig. IV.12). The two grass species had the highest shoot and root weights and the

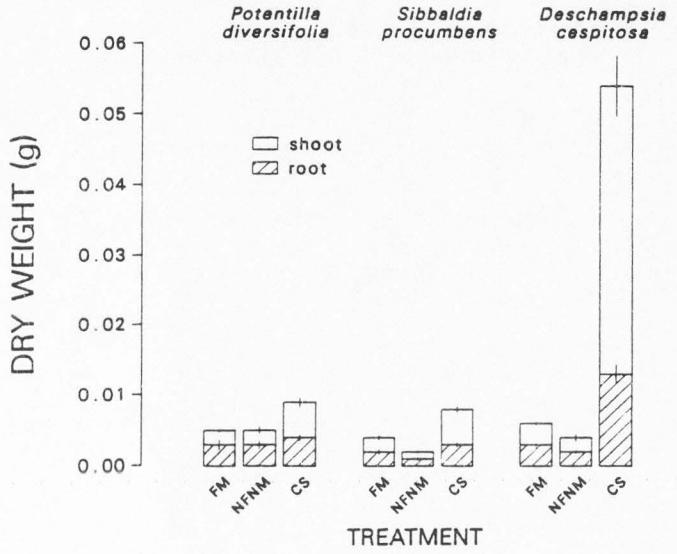

FIG. IV.11. Seedling root and shoot dry weights of individuals that emerged and were harvested in 1986 on fertilized, mulched (FM) and not-fertilized, not-mulched plots (NFNM) on the disturbed area and on cleared, seeded plots (CS) on the undisturbed area, Beartooth Plateau, Montana. Values are means and error bars represent $\pm$ 1 SE; n is variable.

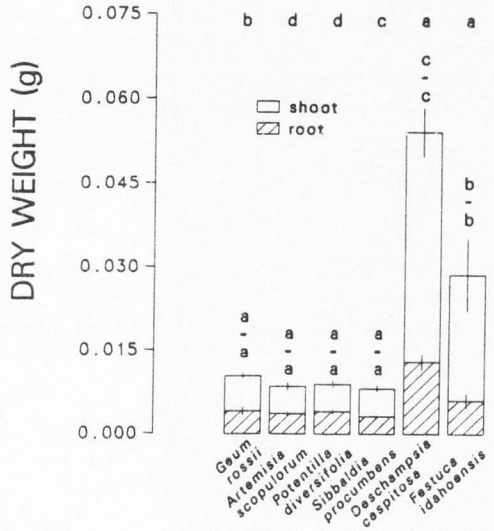

FIG. IV.12. Seedling root and shoot dry weights of individuals that emerged and were harvested in 1986 on the undisturbed area. Values are means and error bars represent ± 1 SE; n is variable. Unlike letters indicate significant differences among species in R/R+S ratios, shoot weights, and root weights for the first, second, and third rows of letters, respectively ($P < .05$).

lowest R/R+S ratios. R/R+S ratios differed significantly among forb species.

Seedling emergence

Seedling emergence on the disturbed area was examined for 1985 and 1986 cohorts 1 and 2 (Table IV.3). Differences among cohorts, fertilizer and mulch treatments, and replications were determined for each species from CDA. The magnitude of difference among and within factors was evaluated from estimated standardized values of interaction u-terms (estimated u-terms divided by estimated standard error) generated by CDA. CDA models required at least all main factors and two-way interactions to explain factor effects for each species, except G. rossii. Therefore, comparisons of collapsed data files (e.g., summed over replications) were not performed.

Late seral species, especially G. rossii and F. idahoensis, had the greatest number of individuals emerge in 1985 cohort 1, and had fewer introductions in successive cohorts. The early seral species, P. diversifolia and D. cespitosa, exhibited more continuous seedling emergence over time. The majority of introductions for ruderal species occurred in the first two cohorts of 1985. The second cohort frequently had as many individuals as the first cohort.

Nonfertilized plots had more introductions than fertilized plots for all late and early seral dominants, except G. rossii. This difference resulted from the exceptionally large numbers of introductions in replication 3 of not-fertilized, mulched plots and is probably not biologically meaningful. Fertilization was a term in CDA

TABLE IV.3. Numbers of introductions of early and late seral dominant and ruderal species on disturbed area. CDA was performed for differences among cohorts (C), fertilizer (F) and mulch (M) treatments, and replications (R) for each species. Terms in the CDA models are for $P < .05$.

	Fertilized mulched			Fertilized not mulched			Not fertilized mulched			Not fertilized not mulched		
	R1*	R2	R3	R1	R2	R3	R1	R2	R3	R1	R2	R3
Late seral dominants												
Geum rossii												
1985 Cohort 1	18	16	20	2	2	0	16	17	38	1	3	0
Cohort 2	0	1	0	0	0	0	0	5	9	0	1	0
1986 Cohort 1	0	0	0	0	0	0	0	1	0	0	0	0
Cohort 2	0	0	0	0	0	0	0	1	1	0	0	0
CDA model terms: C, M, R												
Artemisia scopulorum												
1985 Cohort 1	45	0	32	0	1	0	3	37	82	15	12	0
Cohort 2	26	0	1	2	1	0	9	8	32	3	6	0
1986 Cohort 1	1	6	0	0	0	0	2	6	4	0	0	6
Cohort 2	0	4	0	0	3	5	14	0	2	1	6	1
CDA model terms: C, F, M, R, CF, CM, CR, FM, FR, MR, CFM, CFR, CMR, FMR												
Festuca idahoensis												
1985 Cohort 1	3	10	9	2	0	1	6	8	17	2	1	0
Cohort 2	3	2	2	0	0	0	0	0	3	1	0	0
1986 Cohort 1	0	0	0	0	1	1	1	0	1	0	0	0
Cohort 2	0	0	0	1	1	0	0	1	6	0	0	0
CDA model terms: C, F, M, R, CF, CM, CR, FM, FR, MR												
Early seral dominants												
Potentilla diversifolia												
1985 Cohort 1	47	15	20	1	3	1	2	22	71	5	14	1
Cohort 2	8	1	0	2	0	0	1	0	22	5	2	0
1986 Cohort 1	3	14	0	0	0	0	12	0	0	2	0	4
Cohort 2	0	0	2	0	0	1	17	4	4	14	1	1
CDA model terms: C, F, M, R, CF, CM, CR, FM, FR, MR, CFR, CMR, FMR												
Sibbaldia procumbens												
1985 Cohort 1	2	3	1	0	0	3	0	3	8	2	2	0
Cohort 2	1	0	0	0	0	1	0	1	4	0	0	0
1986 Cohort 1	5	11	8	0	0	1	0	6	4	0	0	10
Cohort 2	44	13	7	4	22	24	0	78	71	31	12	4
CDA model terms: C, F, M, R, CF, CM, CR, FM, FR, MR, CFM, CFR, CMR, FMR												
Deschampsia cespitosa												
1985 Cohort 1	12	14	11	1	7	2	2	17	7	9	5	3
Cohort 2	5	9	4	1	0	0	0	2	16	1	0	1
1986 Cohort 1	9	4	8	0	0	0	2	9	7	0	0	0
Cohort 2	11	5	3	1	3	6	6	5	11	3	3	1
CDA model terms: C, F, M, R, CM, CR, FM, FR, MR, CMR, FMR												

TABLE IV.3. cont.

Ruderal species													
Cerastium arvense													
1985	Cohort 1	11	17	9	13	6	3	6	8	6	21	14	0
	Cohort 2	3	2	0	8	4	0	5	2	4	13	3	0
1986	Cohort 1	0	1	0	1	0	0	0	0	1	0	0	1
	Cohort 2	1	4	0	3	2	3	5	0	3	0	1	0
CDA model terms: C, F, M, R, CF, CM, CR, FM, FR, MR, CFM													
Draba crassifolia													
1985	Cohort 1	11	5	13	63	19	8	5	19	16	24	19	1
	Cohort 2	5	0	2	54	6	6	1	5	29	28	26	0
1986	Cohort 1	1	0	0	0	4	0	1	6	14	3	7	1
	Cohort 2	0	0	0	8	17	3	3	2	7	1	5	0
CDA model terms: C, F, M, R, CF, CM, CR, FM, FR, MR, CFM, CFR, CMR, FMR													
Arenaria obtusiloba													
1985	Cohort 1	41	26	5	23	23	5	16	17	9	7	17	0
	Cohort 2	101	20	4	149	31	3	31	12	14	39	39	2
1986	Cohort 1	4	2	1	6	1	0	2	7	5	7	23	0
	Cohort 2	6	1	0	12	2	4	12	7	5	11	11	3
CDA model terms: C, F, M, R, CF, CM, CR, FM, FR, MR, CFM, CMR, FMR													
Androsace septentrionalis													
1985	Cohort 1	3	1	1	9	11	1	2	4	3	3	10	0
	Cohort 2	0	2	0	12	5	6	3	0	7	6	13	6
1986	Cohort 1	1	3	0	1	0	0	0	0	1	0	5	1
	Cohort 2	3	0	1	2	3	1	8	1	0	2	3	1
CDA model terms: C, F, M, R, CF, CM, CR, FM, FR, MR, CFM, CFR, CMR, FMR													
Draba incerta													
1985	Cohort 1	18	3	1	8	4	2	0	9	4	2	3	0
	Cohort 2	13	1	1	16	2	1	6	1	0	5	6	0
1986	Cohort 1	3	0	1	0	0	1	1	2	0	1	0	0
	Cohort 2	0	1	0	2	1	1	1	1	4	1	1	0
CDA model terms: C, F, M, R, CF, CM, CR, FM, FR, CFM, CFR													

*R = replication.

models for all ruderal species. However, no consistent patterns were observed and detailed comparisons are not warranted as the distribution of the seed pools prior to the study was unknown for these species.

Mulch significantly increased emergence of all early and late seral dominants, but especially that of late seral dominants, F. idahoensis and G. rossii. Wind contributes significantly to soil and litter movement in alpine ecosystems, and these effects are most pronounced on bare soils (Bliss 1985). In this study mulch and netting held both seed and soil in place. Mulching was a significant term in the CDA models for all of the ruderal species, but the distribution of seeds among plots was unknown and detailed comparisons are not justified.

Significant differences existed among replications for both early and late seral dominants. Although the study area was originally chosen for its homogeneity, the erosive forces of wind and water, and consequently the ability to retain seeds, may have differed among plots. In addition, differences in plot installation among replications may have affected establishment. Differences among replications existed for ruderal species with replication 3 having the fewest introductions. Because of the blocked design, this replication was farthest from the edge of the disturbance and may have had the smallest seed pool.

On the undisturbed area, numbers of introductions were evaluated only for 1986 cohorts 1 and 2 (Table IV.4) because of failure of seeded species to establish in 1985 and subsequent reseeding of plots. Seedling establishment of early and late seral dominants was

TABLE IV.4. Numbers of introductions of early and late seral dominant and ruderal species on undisturbed area in 1986. No seedlings of study species occurred on not cleared, not seeded plots. D. crassifolia and A. septentrionalis were not found on the undisturbed area.

	Cleared seeded[+]			Not cleared seeded			Cleared not seeded		
	R1[*]	R2	R3	R1	R2	R3	R1	R2	R3
Late seral dominants									
Geum rossii									
Cohort 1	11	13	13	1	0	0	0	1	0
Cohort 2	1	0	1	0	0	0	0	0	0
Artemisia scopulorum									
Cohort 1	51	63	64	8	1	0	0	0	0
Cohort 2	5	5	11	7	0	0	0	0	0
Festuca idahoensis									
Cohort 1	2	2	7	0	0	0	0	0	0
Cohort 2	1	0	1	1	0	0	0	0	0
Early seral dominants									
Potentilla diversifolia									
Cohort 1	70	66	55	21	1	8	0	0	0
Cohort 2	2	6	5	3	0	0	0	0	0
Sibbaldia procumbens									
Cohort 1	46	50	37	4	0	0	0	0	0
Cohort 2	4	4	5	5	0	0	0	0	0
Deschampsia cespitosa									
Cohort 1	64	100	60	0	0	0	0	0	0
Cohort 2	20	11	8	0	0	0	0	0	0
Ruderal species									
Cerastium arvense									
Cohort 1	3	0	4	0	0	0	0	1	0
Cohort 2	1	1	0	0	0	0	0	0	0
Arenaria obtusiloba									
Cohort 1	19	13	25	0	0	0	1	6	0
Cohort 2	6	2	1	0	0	0	0	0	1
Draba incerta									
Cohort 1	12	43	52	0	0	0	1	5	5
Cohort 2	6	13	15	0	0	0	0	0	3

[+]CDA model terms for comparison of early and late seral dominants, cohorts, and replications within cleared - seeded plots: species, cohorts, replications, and species x cohorts. When ruderal species were included, model terms became: species, cohorts, replications, species x cohorts, and species x replications.

[*]R = replications.

almost entirely restricted to seeded plots cleared or not cleared of vegetation. All three late seral dominants established on seeded, not-cleared plots, but only A. scopulorum had more than one individual. Early seral dominants, P. diversifolia and S. procumbens, also occurred on not-cleared, seeded plots. However, most introductions occurred in replication 3 and local microenvironmental conditions may have facilitated greater establishment. Ruderal species occurred only on cleared plots, regardless of seeding treatment. Greater numbers of ruderals in 1986 cohorts 1 and 2 were found on seeded than unseeded plots because in contrast to seeded plots, unseeded plots were not disturbed during reapplication of the seeding treatment in the fall of 1985.

The majority of emergence for all species on the undisturbed area was on cleared and seeded plots and differences among species, cohorts, and replications within this treatment were examined using CDA (Table IV.4). The largest estimated effects were for species and cohorts. A species by cohort interaction indicated that cohort differences varied among species. For this area, large differences in estimated interaction u-terms due to replication were observed only for D. cespitosa and D. incerta. The smallest numbers of introductions were for two late seral dominants, F. idahoensis and G. rossii, and the ruderal species, C. arvense. The lack of higher numbers of ruderal species was probably a function of a limited seed source. Two ruderals that occurred on the disturbed area, A. septentrionalis and D. crassifolia, were not present on the undisturbed area.

Seedling survival

The data set contained a high proportion of zero values, thus complicating the analyses and perhaps confounding the results. For all late and early seral dominant species, certain cohort-treatment-replication combinations had few or no introductions. This problem was less severe for ruderal species, because the data were summed over subplots within a main plot. With small numbers of introductions, a single death can result in a substantial and nonrepresentational increase in mortality odds. In general, mortality was low and zero values were common. To avoid division by zero in CDA and logit models, a small constant (0.1) was added to both numbers of alive and dead. However, because of the large number of zeros in the data set, calculated mortality odds from logit models did not always accurately reflect the real data set. To minimize this problem, mortality odds from logit models were compared to those from the real data, and large differences were noted. Finally, differences in both establishment and mortality odds existed among replications. Therefore, replications were in all cases treated simply as another main factor.

Because establishment during 1985 and 1986 was extremely low for cohorts 3 and 4, they were excluded from analyses. Species survival of 1985 and 1986 cohorts 1 and 2 summed over replications for the two fertilizer and two mulch treatments on the disturbed area are displayed in Fig. IV.13 (late and early seral dominants) and Fig. IV.14 (ruderal species).

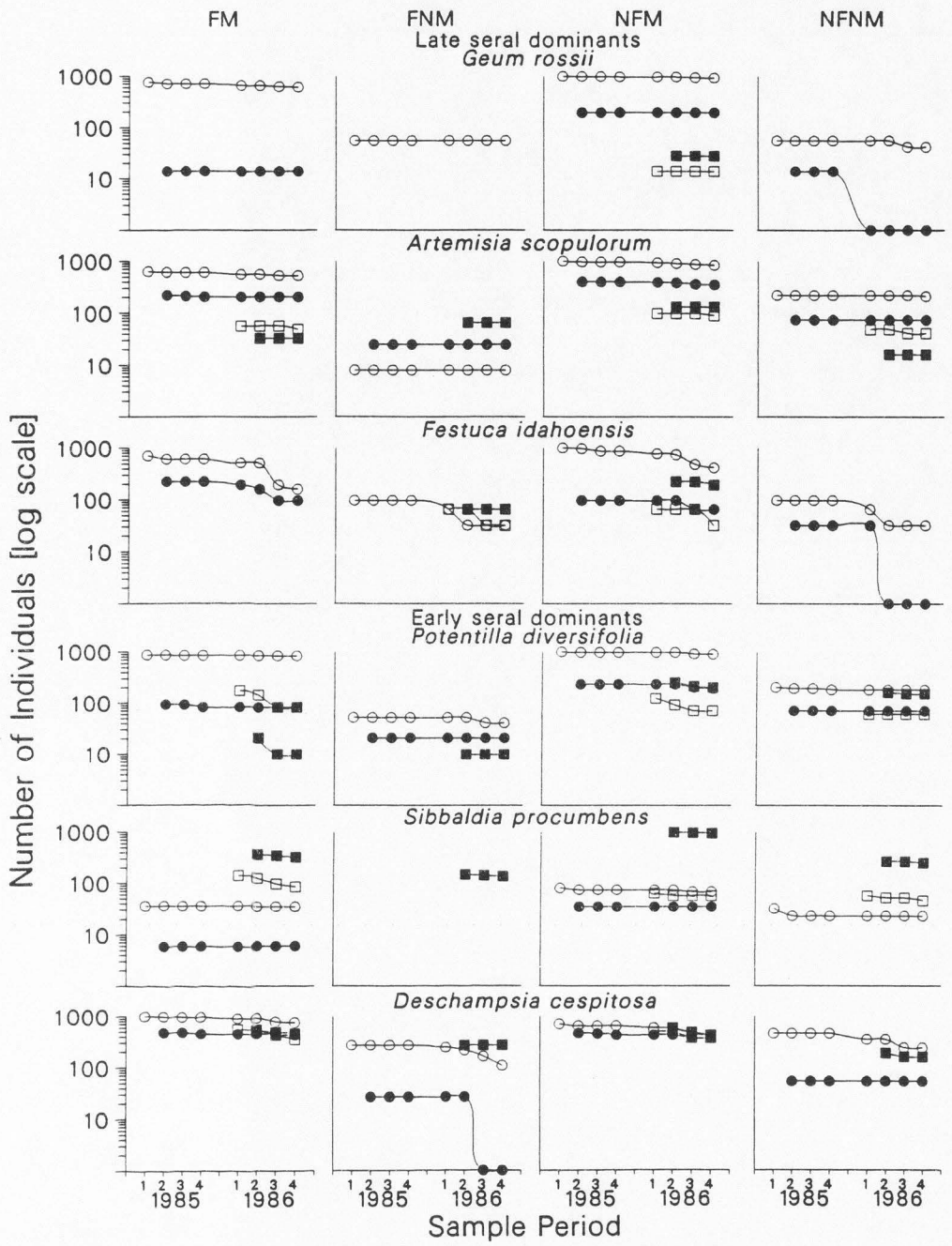

FIG. IV.13. Survival of late and early seral dominants under two fertilizer and two mulch treatments on the disturbed area during 1985 and 1986 on the Beartooth Plateau, Montana. Treatment codes are as in Fig. 4. Values for individual species are relativized across treatments. Open and closed circles are 1985 and 1986 cohorts 1 and 2 and open and closed squares are 1986 cohorts 1 and 2, respectively.

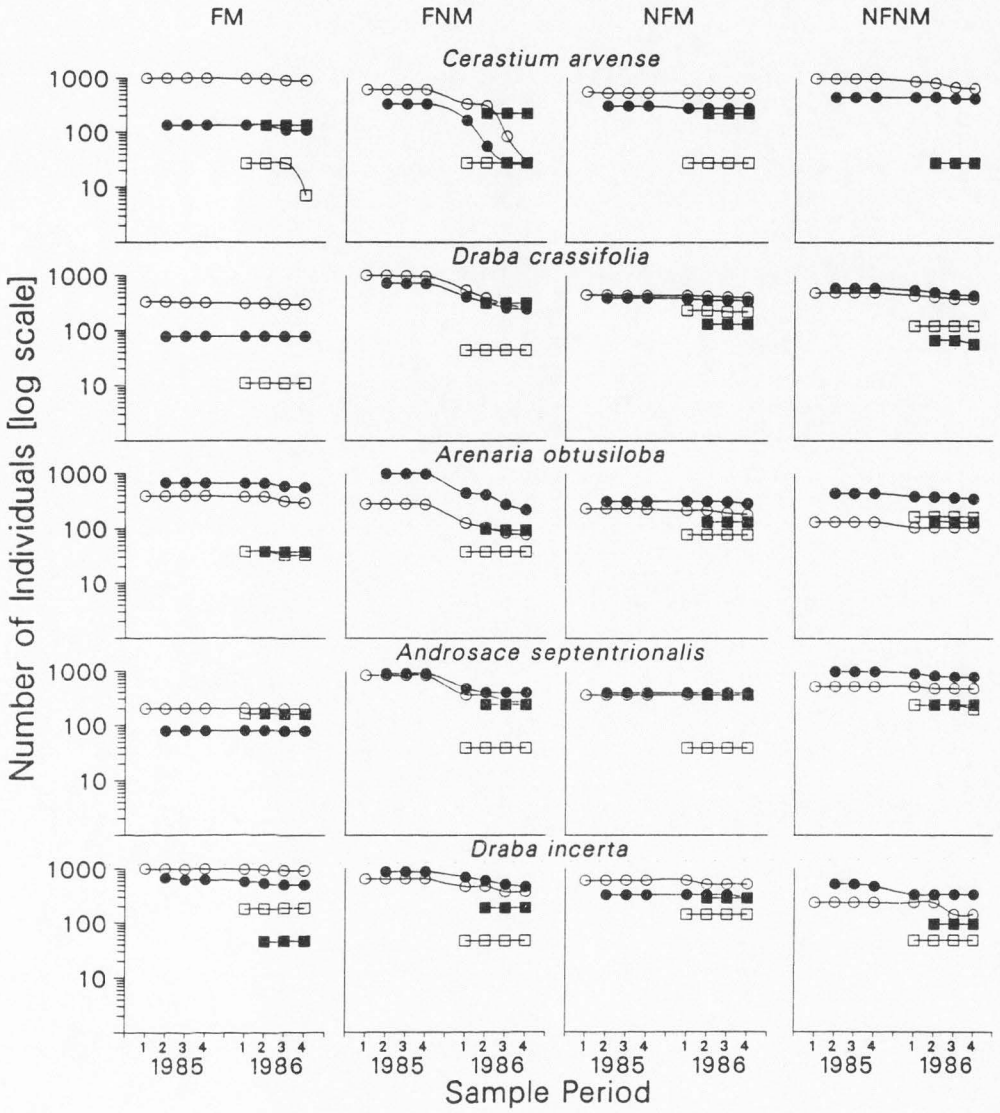

FIG. IV.14. Survival of ruderal species under two fertilizer and two mulch treatments on the disturbed area during 1985 and 1986 on the Beartooth Plateau, Montana. Treatment codes as in Fig. 4. Values for individual species are relativized across treatments. Open and closed circles are 1985 cohorts 1 and 2 and open and closed squares are 1986 cohorts 1 and 2, respectively.

To evaluate differences in log-odds mortality over the two year study period for 1985 cohorts 1 and 2 of the disturbed area, logit models were used that included survival periods, cohorts, fertilizer and mulch treatments, and replications as explanatory variables and number dead vs. alive as response variables. Survival periods were defined as: (1) first year, (2) overwinter, and (3) second year. Inclusion of an explanatory variable in the model indicated a significant effect on the response variable ($P \leq .05$).

In general, log-odds mortality of early and late seral dominant and ruderal species for 1985 cohorts 1 and 2 over all 3 survival periods was low (Table IV.5). Effects of explanatory variables on mortality odds were more consistent for ruderal species than for early and late seral dominants. In general, there was higher mortality on nonmulched than on mulched plots and on fertilized than on nonfertilized plots, with the highest mortality odds occurring on fertilized plots that were not-mulched. An exception was P. diversifolia which had higher mortality on nonfertilized than on fertilized plots. Ruderal species had much larger mortality odds on fertilized plots that were not mulched than did early or late seral dominants. Period x mulch and fertilizer x mulch interactions for C. arvense and A. obtusiloba indicated that the response to mulch was not consistent over either periods or fertilizer treatments for these species. Significant differences in survival periods existed and differences among treatments increased over time. Overwinter mortality odds were frequently higher than first year mortality odds, and second year mortality odds were greater than overwinter mortality odds.

TABLE IV.5. Log-odds mortality of early and late seral dominants and ruderals for 1985 cohorts 1 and 2 on the disturbed area. Logit models (CDA) were used to determine differences among survival periods (P), cohorts (C), fertilizer (F) and mulch (M) treatments, and replications (R), and to calculate log-odds mortality ratios. Odds shown reflect significant model terms except where otherwise indicated. Odds with different letters are statistically different (X^2, $P < .05$).

Late seral dominants						
Geum rossii	Mulched			Not mulched		
	.05			.20		
Artemisia scopulorum	Fertilized			Not fertilized		
	R1*	R2	R3	R1	R2	R3
	.03a	.22bc	.15c	.01ab	.08b	.05ab
Festuca idahoensis	1st year		Overwinter		2nd year	
	.14a		.20a		1.0b	
Early seral dominants						
Potentilla diversifolia	Fertilized			Not fertilized		
	Cohort 1		Cohort 2	Cohort 1		Cohort 2
1st year	.02a		.05bc	.04ab		.10b
Overwinter	.01a		.02a	.01a		.03a
2nd year	.05ab		.12c	.09bc		.23d
Sibbaldia procumbens	Mulched			Not mulched		
	.07			.23		
Deschampsia cespitosa	Mulched			Not mulched		
1st year	.05a			.12a		
Overwinter	.07a			.18b		
2nd year	.23b			.58c		

TABLE IV.5. cont.

Ruderal species	Fertilized		Not fertilized	
	Mulched	Not mulched	Mulched	Not mulched
Cerastium arvense				
1st year	.01a	.02a	.05ab	.01a
Overwinter	.04ab	.60d	.05ab	.10ab
2nd year	.12bc	6.84e	.03a	.24cd
Logit model terms: P, F, M, PF, PM, FM				
Draba crassifolia				
1st year	.02a	.05ab	.01a	.02a
Overwinter	.08ab	.25d	.04ab	.11b
2nd year	.16b	.48e	.07ab	.21c
Arenaria obtusiloba				
1st year	.02a	.02a	.01a	.00a
Overwinter	.03a	1.24c	.02a	.16b
2nd year	.20b	1.21c	.15b	.11b
Logit model terms: P, F, M, PM, FM				
Androsace septentrionalis				
1st year	.01a	.04a	.00a	.01a
Overwinter	.21ab	.79c	.04a	.15ab
2nd year	.11ab	.40b	.02a	.08a

Draba incerta	Mulched	Not mulched
1st year	.02a	.07a
Overwinter	.09a	.27b
2nd year	.12b	.34b

*R = replication.

To determine if first growing season mortality odds differed among years, logit models were used that included numbers of individuals alive vs. dead in September 1985 from 1985 cohorts 1 and 2, and in September 1986 from 1986 cohorts 1 and 2. The explanatory variables were year, cohort, fertilizer and mulch treatments, and replications. Year was the only significant explanatory term in the model for all species, except S. procumbens, for which cohort was the only significant term (Table IV.6). The odds of mortality were higher in 1986 than in 1985 for all species, except G. rossii, which had almost no introductions in 1986. Mortality odds among species were more similar in 1985 than in 1986. F. idahoensis had the highest mortality odds in 1985 and 1986, but two early seral dominants, P. diversifolia and D. cespitosa, also had high mortality odds in 1986. In general, ruderal species had the lowest mortality odds during both years.

S. procumbens had higher mortality for 1985 and 1986 cohorts 1 than 2. Larger numbers of introductions in cohort 2 of 1986 may have resulted in more reliable estimates.

Effects of treatments and replications on the disturbed area after two growing seasons were examined with log-odd mortalities calculated from total number of individuals dead vs. alive in September 1986. Values were summed over 1985 and 1986 cohorts 1 and 2. Logit models included only fertilizer and mulch treatments, and replications as explanatory variables. Among the late seral dominants, G. rossii had higher mortality odds on nonmulched than on mulched plots (Table IV.7). In addition, F. idahoensis and A. scopulorum had higher mortality odds on fertilized than on

TABLE IV.6. First year mortality odds for 1985 and 1986 cohorts 1 and 2 on the disturbed area. Logit model (CDA) comparisons included year, cohort, fertilizer and mulch treatment, and replications. Year was the only significant model term for all species, except S. procumbens, for which cohort was the significant model term.

	1985	1986
Late seral dominants		
Geum rossii	.07	.00
Artemisia scopulorum	.04	.12
Festuca idahoensis	.14	.44
Early seral dominants		
Potentilla diversifolia	.04	.39
Deschampsia cespitosa	.07	.28
Ruderal species		
Cerastium arvense	.02	.08
Draba crassifolia	.02	.05
Arenaria obtusiloba	.01	.05
Androsace septentrionalis	.02	.09
Draba incerta	.04	.10

Early seral dominant	Cohort 1	Cohort 2
Sibbaldia procumbens	.33	.05

TABLE IV.7. Log-odds mortality of individuals of early and late seral dominants and ruderals on the disturbed area in September 1986. Values were summed for 1985 and 1986 cohorts 1 and 2. Logit models (CDA) were used to determine differences among fertilizer (F) and mulch (M) treatments and replications (R), and to calculate log-odds. Odds shown reflect significant model terms except where otherwise indicated. Odds with different letters are statistically different (X^2, $P < .05$).

Late seral dominants						
Geum rossii	Mulched			Not mulched		
	R1*	R2	R3	R1	R2	R3
	.01a	.05a	.19b	.03a	.20b	.80b
Artemisia scopulorum	Fertilized			Not fertilized		
	R1	R2	R3	R1	R2	R3
	.04a	.27b	.34c	.02a	.15b	.19b

Festuca idahoensis	Fertilized		Not fertilized	
	Mulched	Not mulched	Mulched	Not mulched
R1	.36ab	.00a	1.77bc	.99ab
R2	1.62ab	.00a	1.07ab	.00a
R3	11.39c	6.39bc	.94ab	.00a

Early seral dominants *Potentilla diversifolia*	Fertilized		Not fertilized	
	Mulched	Not mulched	Mulched	Not mulched
R1	.06ab	.14bc	.19c	.00a
R2	.38c	.00a	.15bc	.07ab
R3	.09ab	.20bc	.10abc	.05ab

Sibbaldia procumbens	Fertilized	Not fertilized
	.12	.06

Deschampsia cespitosa	Fertilized		Not fertilized	
	Mulched	Not mulched	Mulched	Not mulched
	.27a	.37a	.39a	.54a

TABLE IV.7. cont.

Ruderal species	Fertilized		Not fertilized	
	Mulched	Not mulched	Mulched	Not mulched
Cerastium arvense				
1st year	.01a	.02a	.05ab	.01a
Overwinter	.04ab	.60d	.05ab	.10ab
2nd year	.12bc	6.84e	.03a	.24cd
Logit model terms: P, F, M, PF, PM, FM				
Draba crassifolia				
1st year	.02a	.05ab	.01a	.02a
Overwinter	.08ab	.25d	.04ab	.11b
2nd year	.16b	.48e	.07ab	.21c
Arenaria obtusiloba				
1st year	.02a	.02a	.01a	.00a
Overwinter	.03a	1.24c	.02a	.16b
2nd year	.20b	1.21c	.15b	.11b
Logit model terms: P, F, M, PM, FM				
Androsace septentrionalis				
1st year	.01a	.04a	.00a	.01a
Overwinter	.21ab	.79c	.04a	.15ab
2nd year	.11ab	.40b	.02a	.08a

Draba incerta	Mulched	Not mulched
1st year	.02a	.07a
Overwinter	.09a	.27b
2nd year	.12b	.34b

*R = replication.

not-fertilized plots. All of the late seral dominants showed significant differences among replications. Early seral dominants also exhibited a significant response to fertilizer. However, S. procumbens had higher mortality odds on fertilized than nonfertilized plots, D. cespitosa showed higher mortality odds on not-fertilized than fertilized plots, and results for P. diversifolia were highly confounded by replication effects. The logit models showed significantly higher mortality odds for D. cespitosa on not-mulched than on mulched plots, but these differences were not significant using chi-square comparisons. P. diversifolia also had significant differences among mulching treatments; these differences were confounded with replications.

Ruderal species exhibited more consistent mortality patterns than did early or late seral dominants. Ruderals generally had higher mortality odds on nonmulched plots than on mulched plots. In addition, the highest mortality odds occurred on fertilized plots, specifically on fertilized, nonmulched plots. Three ruderal species, D. crassifolia, A. obtusiloba, and D. incerta, had significant differences among replications, which may have been largely attributable to replication 1 of the fertilized, not-mulched treatment. This particular replication had melt-water running through it early in the second growing season, and may have experienced a higher incidence of needle ice than other plots.

On the undisturbed area, only cleared and seeded plots had all of the seeded species establish. Survival of species that established on this plot is shown in Fig. IV.15. A logit model that included species, cohorts, and replications as the explanatory variables,

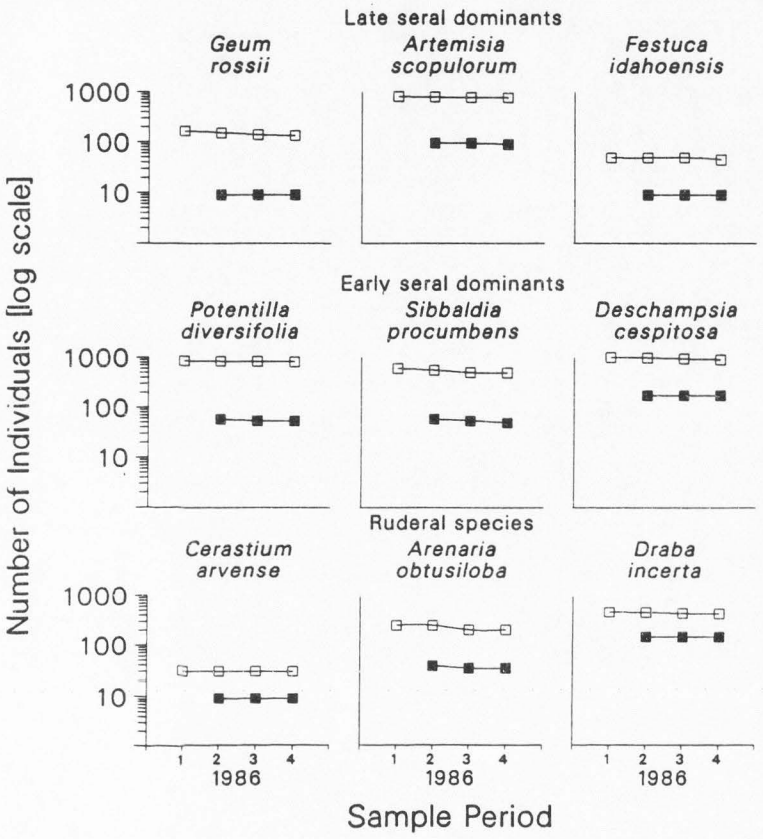

FIG. IV.15. Survival of late and early seral dominant and ruderal species on cleared and seeded plots on the undisturbed area in 1986 on the Beartooth Plateau, Montana. Values are relativized across species. Open and closed squares are 1986 cohorts 1 and 2, respectively.

showed that only species had a significant effect on the response variable (Table IV.8). In general, mortality odds were low, ranging from .05 to .22. No consistent patterns of mortality were observed among late or early seral dominant or ruderal species. The highest mortality odds were for late seral dominant, G. rossii, early seral dominant, S. procumbens, and ruderal species, D. incerta. The lowest mortality odds also occurred in all three successional categories and included the species, A. scopulorum, P. diversifolia, and D. incerta.

Mortality odds for species that established on seeded, cleared and not-cleared plots of the undisturbed area were examined with a logit model that included species, cohorts, clearing treatment, and replication as the explanatory variables (Table IV.9). There were no differences in mortality odds among cleared plots and not-cleared plots or cohorts. Species and replications were the only significant terms in the model. P. diversifolia generally had lower mortality odds than A. scopulorum or S. procumbens, and S. procumbens had higher mortality odds than the other two species.

DISCUSSION

Effects of disturbance type on seedling environment

The effects of disturbance type on soil nutrients, temperature, and water potential were similar to those observed on disturbances of different magnitude in more temperate ecosystems (Chapin 1983, Bazzaz 1983, Vitousek 1985). The gap-type disturbance within the native Geum turf area that had vegetation removed but surface soil horizons left

TABLE IV.8. Mortality odds of early and late seral dominant and ruderal species on undisturbed area, seeded-cleared plots in September 1986. Values are for 1986 cohorts 1 and 2. Logit model (CDA) comparisons included species, cohorts, and replications; species was the only significant model term. Values with different letters are statistically different (X^2, $P < .05$).

Late seral dominant	
Geum rossii	.16bc
Artemisia scopulorum	.05a
Festuca idahoensis	.13abc
Early seral dominant	
Potentilla diversifolia	.05a
Sibbaldia procumbens	.22c
Deschampsia cespitosa	.09ab
Ruderal species	
Arenaria obtusiloba	.22c
Draba incerta	.06ab

TABLE IV.9. Mortality odds for 1986 cohorts 1 and 2 on seeded, cleared and not-cleared plots of the undisturbed area in September 1986. Logit model comparisons were among species, cohorts, clearing treatment, and replications. Species and replication were the significant model terms. Odds with different letters are statistically different (X^2, $P < .05$).

	R1*	R2	R3
Late seral dominant			
Artemisia scopulorum	.11bc	.04a	.10b
Early seral dominant			
Potentilla diversifolia	.06a	.02a	.06ab
Sibbaldia procumbens	.30c	.10bc	.28bc

*R = replication.

in place exhibited higher levels of available N and P than vegetated plots within the same community. This was indicative of higher rates of decomposition and mineralization and of little uptake by seedlings (Matson and Vitousek 1981). Levels of nutrients available to developing seedlings were also higher on the gap-type disturbance than on the severe disturbance, because nutrient pools and cycling capacities of the well-developed peat soils on the undisturbed area were apparently greater than those of the mineral soils on the severely disturbed area (Chapin 1983). Differences among treatments were measured only once, during August of the second year after plot installation; levels of nutrients are known to fluctuate during the growing season in tundra ecosystems (Everett et al. 1981, Haselwandter et al. 1983, Chambers et al. 1987a). Nutrient levels in cleared and vegetated plots may be more similar at the beginning of the growing season, as spring runoff usually induces a nutrient pulse that is followed by a gradual decrease in nutrient levels during periods of active plant growth.

Soil temperatures were higher on cleared than vegetated plots on the undisturbed area, especially at 5 and 15 cm. Removal of insulating vegetation frequently results in greater radiation loads on the soil surface and a concomitant increase in soil temperature (Cochran 1969, Vitousek 1985). Change in temperature following disturbance can alter nutrient availability (Chapin and Bloom 1976) and may have contributed to higher rates of mineralization on cleared plots. The higher soil temperatures observed on undisturbed area cleared plots than on disturbed area plots were a function of differences in soil thermal properties. On clear days soil surface

temperatures in excess of 40°C were measured on cleared plots on the undisturbed area, while surface temperatures on severely disturbed plots were routinely 10°C lower. The peat soils of the undisturbed area are characterized by lower thermal conductivities, heat capacities, thermal diffusivities, and thermal contact coefficients than the sandy loam soils of the disturbed area (Cochran 1969). The net effect on the seedling environment is large diurnal fluctuations in soil surface temperatures, and generally higher soil temperatures at shallow depths during periods of moderate to high solar radiation. In contrast, the seedling environment on the severely disturbed area has smaller daily temperature fluctuations, but cooler temperatures during periods of high insolation. The most favorable environment for seedlings may be on the gap-type disturbance during cool, overcast days and on the severely disturbed area during warm, cloudless days.

Disturbance type, i.e., gap or severe, had little effect on soil water potential. However, vegetated plots on the undisturbed site experienced lower soil water potentials during the mid to late growing season in 1985 and 1986 than either of the plot types from which vegetation had been removed. Plant water stress during the growing season in alpine ecosystems has been measured in mature individuals in the Geum turf vegetation type (Ehleringer and Miller 1975, Johnson and Caldwell 1975) and is implicated as one of the major causes of mortality in alpine and arctic seedlings (Bonde 1968, Bliss 1971, Bell and Bliss 1980). The soil moisture stress (< -1.5 MPa) observed in other alpine ecosystems during August and September (Bell and Bliss 1979, Klikoff 1965) did not occur during this study at either 5 or 15 cm. Seedling root lengths ranged from 3 to 6 cm after the first

growing season and from 8 to 19.5 cm and second growing season. Any water stress experienced by seedlings probably occurred early in the first growing season shortly after germination.

The combined effects of high soil temperature and low surface water potentials early in the growing season may, in part, explain the lack of seedling emergence on the undisturbed area in 1985. Low precipitation and high ambient temperatures early in 1985 resulted in extremely high soil surface temperatures on undisturbed plots that were cleared of vegetation. Surface soil water potentials may also have been quite low during this period and mortality of germinating seedlings was probably high.

The importance of growing season conditions on seedling environment has been stressed for numerous ecosystems (Bazzaz 1983). Differences in climatic conditions on the Beartooth Plateau during 1985 and 1986 had a large effect on seedling environment (Table IV.10).

Effects of fertilizer and mulch on seedling environment

Levels of available N (NO_3 and NH_4) and P were higher in fertilized than in not-fertilized plots on the disturbed area two years after fertilization, but only about one-half the amount of P and less than one-tenth the amount of N originally applied were still present in the soil. Sandy loam soils, such as those on the disturbed area, are characterized by high porosities, low cation exchange capacities, and consequently, low nutrient retention (Tisdale and Nelson 1975). Regardless of soil type, rapid declines in nitrogen

Table IV.10. Differences in climatic variables in 1985 and 1986 on the Beartooth Plateau, Montana and effects on seedling environment during the growing season.

	1985	1986
Growing season	Longer, early snowmelt	Shorter, Late snowmelt
Precipitation	Less overall; dry early in growing season	More overall, wet early in growing season
Air Temperature	Warmer early in growing season	Cooler early in growing season
Soil Water Potential	Drier early; especially on vegetated plots	Very wet soils early
Soil Temperatue	Warmer early in growing season	Cooler early in growing season

levels following fertilization are common. To minimize these losses, nitrogen was applied as ammonium instead of nitrate because of its lower mobility in the soil. However, after two years it is likely that most of the ammonium had been converted into the more mobile nitrate anion and leached from the soil. The effect of nitrogen fertilization on the seedling environment was probably a pulse of nitrogen at the beginning of the first growing season as soil temperatures warmed and ammonium was converted to nitrate, followed by a gradual decline during the remainder of the growing season due to increased precipitation and leaching losses. Further losses probably occurred in these sandy soils at the initiation of the second growing season during spring runoff. Higher levels of phosphorous in fertilized plots may reflect the immobility of the phosphate anion and its tendency not to be leached from soil. As a result, phosphorous availability to seedlings was possibly more constant over time than was that of nitrogen.

The beneficial effects of mulch for seedling establishment in tundra ecosystems has been documented for naturally occurring organic mulches (Bell and Bliss 1980) and for artificially applied straw mulches (Brown et al. 1976, 1978). Mulches can decrease evaporation, resulting in higher water potentials at the soil surface. Soil surface temperature variation may increase, as most mulches have lower thermal conductivities, volumetric heat capacities, and thermal diffusivities than the underlying soil (Cochran 1969). When mulch is incorporated into soil, carbon:nitrogen ratios are usually increased. This results in lower nitrogen availability as nitrogen becomes tied up in microbial biomass during decomposition of the mulch (Tisdale and

Nelson 1975). In this study, mulching had no measured effect on soil water potential or nutrients. Mulch was not incorporated into the soil and little apparent surface decomposition occurred. Mulching did increase soil surface temperatures, but only during the first year after application and then only on sunny days.

Wind is an omnipresent factor in alpine environments and is frequently most intense on soil surfaces bare of vegetation (Bliss 1985). In this study wind had a significant effect in the removal and redistribution of mulch from treated plots. Redistribution of mulch by wind probably resulted in small scale variation in both soil surface water potentials and temperatures that was not measured. Field observations of soil movement on mulched and not-mulched plots strongly suggest that the most important effect of mulch was in preventing surface soil erosion and seed removal by wind. These observations were substantiated by greater numbers of introductions on mulched plots. Seed removal by wind may have been greatest for large seeded late seral dominants, G. rossii and F. idahoensis. Mean seed lengths, including awns, were 7.9, 1.8, 8.7, 1.5, 1.5, and 4.7 mm for G. rossii, A. scopulorum, F. idahoensis, P. diversifolia, S. procumbens, and D. cespitosa, respectively. On bare soil seed characteristics important for incorporation of seed into soil include small seed size, and a lack of appendages or large hairs (Grime et al. 1981). All of the seeded species, except G. rossii and F. idahoensis, had these characteristics and may have been less susceptible to movement by wind.

Seedling growth response to disturbance type and nutrient addition

Two primary determinates of tundra plant growth are air and soil temperatures and soil nutrients (Warren Wilson 1966, Chapin 1981). These factors appeared to have the greatest effect on seedling growth in the current study. The gap-type disturbance was characterized by higher soil nutrient levels and warmer soil temperatures in 1986 than fertilized or not-fertilized plots on the severely disturbed area, and produced larger seedlings than either fertilization treatment on the disturbed area. Seedling growth on the disturbed area was greater in fertilized plots than not-fertilized plots under an identical soil temperature regime. Finally, first year seedling growth on the disturbed area was greater in 1985 than in 1986 on both fertilized and not-fertilized plots, indicating that warmer air and soil temperatures in 1985 had a positive effect on plant growth. In other alpine areas air temperature plus soil temperature has been shown to be significantly correlated with shoot growth and shoot production of tundra graminoids (Bliss 1966), and with shoot and root net production of species from a mesic site (Scott and Billings 1964).

Seedling growth in tundra environments is extremely slow (Wager 1938, Billings 1974). Depending upon species and treatment, growth increments ranged from less than .005 g to about .04 g dry weight during the first growing season and from about .02 g to .20 g during the second growing season. In general, seedling growth was slightly greater for early seral than for late seral dominants. This was especially evident for D. cespitosa which had high growth rates during both growing seasons. S. procumbens and P. diversifolia exhibited a

similar trend by the end of the second growing season. These results agreed with a greenhouse study that examined growth responses and nutrient uptake characteristics of an early seral dominant, D. cespitosa, and a late seral dominant, G. rossii, in a factorially designed experiment with four levels of N and P (Chapter III). In the greenhouse study, relative growth rates of D. cespitosa were greater than those of G. rossii for all combinations of N and P.

Fertilization of severely disturbed plots had no effect on R/R+S ratios of either early or late seral dominant species. These results were contrary to the greenhouse experiment that examined the response of D. cespitosa and G. rossii to levels of N and P (Chapter III). Both species exhibited higher R/R+S ratios at low nutrient levels, although G. rossii responded primarily to levels of P while D. cespitosa was most sensitive to N. In the field study, nutrient addition resulted in a proportionate increase in both roots and shoots. Harvest methods may have resulted in a slight decrease in R/R+S ratios overall, but it is unlikely that this affected the ability to detect treatment differences. Factors other than N and P may be limiting in this alpine ecosystem. Alpine plant root systems have the important functions of absorption, storage of reserves, anchorage, and vegetative reproduction in a cold environment (Daubenmire 1941).

It has been assumed that tundra plants devote a major portion of the first years photosynthate to root system establishment (Billings and Mooney 1968, Billings 1974, Roach and Marchand 1984). This hypothesis has been based primarily on comparisons of root length relative to shoot size (Billings and Mooney 1968, Roach and Marchand

1984). In this study, total root length varied among species and treatments, but ranged from 3 to 6 cm for first year seedlings and from 8 to 19.5 cm for second year seedlings. R/R+S ratios for both years were lower than those that have been measured for mature alpine plants grown under field conditions. R/R+S ratios derived from actual dry biomass data showed that allocation to roots and shoots ranged from approximately .30 to .65 for the various species and treatments. Values of .67 to .86 (2 to 6 times more belowground than aboveground biomass) have been given for perennial alpine dicots (Mooney and Billings 1960, Scott and Billings 1964). Even higher ratios were reported for plants of differing growth forms along an environmental gradient on Niwot Ridge, Colorado, USA (Webber and May 1977). The root systems of mature alpine plants are perennating structures that have developed over a period of years. Establishing seedlings are dependent upon aboveground portions of the plant to produce the necessary photosynthate for growth of both roots and shoots. Root extension may be critical for the survival of alpine seedlings, but a much greater allocation of photosynthate to roots than shoots may result in decreased growth rates and greater susceptibility to the stresses of the environment.

The smallest R/R+S ratios for all harvest dates were for early seral dominants, D. cespitosa and S. procumbens. These results are similar to the greenhouse experiment, as D. cespitosa had smaller R/R+S ratios than G. rossii for all but the lowest levels of N and P (Chapter III). In general, growth differences between early and late seral species were consistent with predictions that relate species responses to nutrient levels as these change during succession (Grime

1977, Chapin 1980, 1983). Early seral dominants, except P. diversifolia, exhibited both higher relative growth rates and lower R/R+S ratios than late seral dominants.

Factors affecting seedling emergence

On the severely disturbed area, factors affecting seedling emergence were dependent upon species successional affinity. Emergence of seeded early and late seral dominants was largely determined by the presence or absence of the mulching treatment. Ruderal species emergence was influenced by the effects of redisturbing the soil when the study was installed. Higher numbers of ruderals emerged in 1985, the year immediately following plot installation, than in 1986.

The early seral dominants, especially S. procumbens, exhibited delayed germination of a significant portion of the seed population. Similar results have been observed for other early seral dominant alpine species, Arenaria groenlandica and Juncus trifidus, in the White Mountains, New Hampshire, USA (Marchand and Roach 1980). A preliminary laboratory experiment examined germination of early and late seral dominants from the current study under light or dark conditions following wet or dry cold-stratification (Chapter II). Early seral dominants, P. diversifolia and D. cespitosa, showed slightly lower overall germination across treatments in the laboratory. This pattern was reflected in the continuous germination observed in the field. Field germination of S. procumbens occurred primarily in the second year after seeding. This was indicative of

some form of innate dormancy and paralleled the lab results in which maximum germination obtained after 32 dy for any treatment was only about 50%. It has been suggested that for annuals to survive in an environment with a high probability of failure, that the seed must remain viable over time with a small percentage of the seed population germinating anually (Cohen 1966). These requirements may also apply for early seral dominants in alpine environments (Billings 1974, Marchand and Roach 1980).

The ability of seedlings to establish on the undisturbed area was greatly affected by clearing treatment. Few seedlings of either late or early seral dominants were found on vegetated plots, and no seedlings of ruderal species were observed. Experimentally sowing seeds into mature Calluna heath and adjacent disturbed areas showed that few species established in the mature vegetation and that establishment was ten times more likely on naturally disturbed areas (Miles 1973). Establishment of seedlings in mature vegetation is rarely observed; this has been attributed to competition for resources (King 1977). The lack of ruderal species in mature vegetation suggests that these species are poor competitors (Gross and Werner 1982). The occurrence of early seral forbs on the vegetated plots is somewhat surprising, and may be attributed to micro-spatial heterogeneity (Silvertown 1981) or greater competitive ability than was originally assigned to these species.

Seedling survival

Several assumptions were implicit in the design of the seedling survival experiment. It was assumed that all germinating individuals were not only observed, but that they were observed during the next sampling period after emergence. The growing season began earlier in 1985 than expected, and seedlings that emerged and died prior to the first sampling period were not censused. In addition, seedlings that germinated and died between sampling periods were not recorded. On the mineral soils of the severely disturbed area, seedlings were sometimes obscured by pebbles and did not become apparent until they had reached a fairly large size. Also, locating seedlings in mulched plots under two layers of Conwed netting and in vegetated plots was a difficult task and some may have been missed. It was assumed that causes of mortality were attributable to factors measured or observed during the course of the study. Evidence existed that needle ice occurred on saturated plots at the beginning of the growing season in 1986, but it was impossible to quantify the effects. Caterpillars were observed on some of the disturbed area plots in 1986, and insect herbivory may have resulted in some seedling mortality. However, insect densities were very low, and mortality due to herbivory was believed to be minimal.

Demographic studies that have examined the mortality of seedlings and juvenile plants usually find concave survivorship curves, indicating a period of high risk early in the life of the plant (Cooke 1979). Studies of seedling survival of alpine plants routinely show mortality values of greater than 50% (mortality odds = 1.0) during the

first growing season (Bonde 1968, Jolls and Bock 1983, Roach and Marchand 1984). In this study, mortality odds of .50 were never exceeded during the first growing season, and were only rarely exceeded after two growing seasons.

Seedling mortality odds were higher on the severely disturbed plots than on cleared plots on the undisturbed area for all species examined, except D. crassifolia. The gap-type disturbance was characterized by a more favorable soil nutrient regime, warmer soil temperatures, and consequently, larger seedlings than either fertilized or not-fertilized plots on the severely disturbed area. The comparison between disturbance types was made only for 1986 which had cooler growing season conditions than 1985. During cool periods the thermal characteristics of the highly organic soils on the gap-type distrubance and resultant higher soil temperatures may improve seedling survival.

Mulch increased survival of most early and late seral dominants and of ruderal species, despite no measured effects on soil nutrients, water potential, or temperature. The effects of wind in redistributing mulch have been noted. It may be that micro-environmental variation created by the patchy distribution of the mulch resulted in microsites that favored seedling survival. The importance of microsite conditions for seedling survival has been observed in alpine (Jolls and Bock 1983) and arctic tundra (Bell and Bliss 1980). Mulch, even if patchy, may significantly ameliorate the deleterious effects of wind by acting as a buffer. This can improve the physiological status of plants by decreasing transpiration and allowing higher leaf temperatures. Also, the physical effects of wind

can be lessened by decreasing soil movement, and consequently, plant abrasion and root exposure (Cochran 1969).

In general, fertilization resulted in increased mortality odds of early and late seral dominant species, except D. cespitosa which had decreased mortality. These results were inconsistent due to small sample sizes and large differences among replications. For ruderal species, fertilization clearly resulted in increased mortality, with the greatest mortality occurring on not-mulched plots. Individuals of all successional types had greater biomass on fertilized plots, an attribute that normally results in lower mortality (Cooke 1979). Slow growth has been suggested as one of the primary causes of mortality in tundra seedlings (Wager 1938, Bell and Bliss 1980), and it is contradictory that the largest seedlings suffered the highest mortality. The higher mortality on fertilized plots may have resulted from an initial pulse of N and P, followed by a rapid decline in N due to leaching from the system. Biomass was not measured for the ruderal species, but their response may have been similar to that of G. rossii and D. cespitosa under increased nutrient levels in the greenhouse experiment, i.e., an increase in the proportion of biomass allocated to shoots (Chapter III). Even if the increase in root and shoot weights was proportional, the larger biomass may have created plant nutrient demands in excess of soil nutrient availability during the second growing season. Ruderal species typically exhibit flexible responses to increases in nutrients. Declines in fertility following a nutrient pulse can result in decreased nutrient absorption, photosynthesis, and growth and, in turn, cause greater susceptibility to other stresses (Chapin 1980). An alternative explanation may be

that the short-lived ruderal species had earlier reproduction on fertilized plots and that plants died soon after setting seed. However, examination of reproduction data collected when the seedlings were mapped showed that increased mortality on fertilized plots was not attributable to earlier reproduction.

Growing season conditions are an important determinate of seedling mortality (Cooke 1979, Bazzaz 1983). Higher mortality was observed in 1986 than 1985 for both first and second year cohorts. The effects of the cooler growing season were not ameliorated by either fertilizer or mulch. For first year cohorts, overwinter mortality was frequently higher than first year mortality and second year mortality greater than overwinter mortality.

Disturbance/Succession Relationships

Disturbance is an important factor in structuring vegetation pattern in alpine landscapes. On Niwot Ridge, Colorado, USA, it has been estimated that pocket gophers (Thomomys talpoides) physically disturb 4.0 ± 7.1 $t \cdot ha^{-1} \cdot yr^{-1}$ of soil (Thorn 1982). Cryopedogenic movement also contributes to the amount of soil disturbed on an annual basis in alpine ecosystems (Johnson and Billings 1962). Factors affecting plant colonization processes following such disturbance have a large impact on alpine plant community composition and richness (Fox 1981). Disturbance can serve as a source of spatial heterogeneity with the intensity of individual disturbances and total area disturbed significantly impacting species diversity (richness and evenness) (Bazzaz 1983, Denslow 1980, 1985).

Several predictions made at the studies' initiation concerning seedling establishment on different alpine disturbance types were not verified. Generally low mortality of all species examined indicates that the alpine environment is not as inhospitable to seedling establishment as previously believed. The fact that early and late seral dominant and ruderal species had low mortality on both severe and gap disturbance types suggests that seedlings of these species growing without competition have wider ranges of adaptability than is typically ascribed to species with different successional affinities. The broad range of adaptability observed is contrary to Grime's (1977, 1979) categorization of competitive species as those occurring in productive environments and ruderal species as those occurring in potentially productive environments.

The ability of early and late seral dominants to survive on both disturbance types indicates that successional processes following disturbance in this alpine ecosystem are described by the initial floristics of Egler (1954) or the tolerance model of Connell and Slatyer (1977). This model states that individuals of any species arriving on a disturbed area that can survive there as adults can become established.

One of the primary determinants of seedling establishment on the two types of disturbed sites appeared to be the ability of seeds to disperse to an area and then to become incorporated into the soil. Despite establishment and survival in the seeding experiments, few early or late seral dominants established on either disturbance type from naturally occurring seeds. In contrast, more species of ruderals occurred naturally on the severe disturbance and in much higher

numbers than either early or late seral dominants. Fewer species of ruderals established on the gap disturbance than on the severe disturbance and densities were lower. One explanation for these establishment patterns is that species from the various successional stages have different reproductive and dispersal characteristics. Reproduction of all alpine species appears to be episodic (Billings 1974). However, reproductive rates of late seral dominants are lower than those of early seral dominants or ruderals, and the seeds of late seral dominants are relatively shorter-lived (J. C. Chambers, unpublished data). In addition, the sizes and shapes of seeds of certain late seral dominants, e.g., G. rossii and F. idahoensis, are not conducive to burial in soil. These factors may result in a paucity of disseminules of late seral dominants in the seed pool regardless of disturbance type. Early seral dominants have relatively higher reproductive rates and longer-lived seeds (J. C. Chambers, unpublished data). The lack of early seral dominants on the disturbed areas may be due to a patchy distribution within the mature community, and a low probability of dispersal to a new gap. The alpine ruderals studied possessed most of the life history characteristics found in temperate ruderals, including short life spans, high growth rates, small seed size, high fecundity, and early reproduction (Grime 1977). More effective dispersal mechanisms may have accounted for the greater abundances of ruderals on the severely disturbed area. The absence of several of the ruderal species in the gap disturbance may have resulted from lack of ruderals in surrounding vegetation and a low probability of dispersal to the gap.

A second explanation for the observed establishment patterns is that the soil surface characteristics of a disturbed area determine the numbers and types of seeds that are "trapped" in the soil. In windy environments, soils with large particle sizes (i.e., sand or gravel) may incorporate greater numbers of seeds than soils with small particle sizes (i.e., loams or peats). The lack of establishment of early and late seral dominant species from naturally occurring seeds on the gap disturbance type may have partly resulted from an inability of seeds falling onto the peat soil to be buried deeply enough to avoid removal by wind. Species that were seeded onto the gap disturbance type were mixed with soil and thus adequately buried. Seed attributes, including size, shape, and presence or absence of appendages, may determine the degree to which seeds of different species are incorporated into soils with varying particle sizes. Large seeded late seral dominants had proportionately greater emergence on the severely disturbed area when protected from wind erosion by mulch and Conwed netting than did the smaller seeded early seral dominants.

If early and late seral and ruderal species can establish on both severe and gap disturbance types and if soil surface properties can determine establishment patterns, it appears that the antithesis of relay floristics (Egler 1954) or the facilitation model (Connell and Slatyer 1977) exists. Given that dispersal is not limiting, greater numbers of seeds are more likely to be incorporated into less-developed soils with large particle sizes than into well-developed soils with small particle sizes. Large seeds may be more readily incorporated into soils with large particle sizes than

into those with small particle sizes. Because late seral dominants often have larger seeds than early seral dominants or ruderals, this implies that seeds of late seral species are more easily incorporated into the frequently less-developed soils of severely disturbed sites than into the often well-developed soils of gap disturbance types. Other factors also affect seed burial in the soil, and these ideas require testing.

This study emphasizes the importance of examining seedling establishment when evaluating successional processes, and lends credence to empirical techniques such as overseeding and transplanting. To accurately determine successional processes, it is necessary to consider all of the life history stages of the study organism under controlled conditions. Simple observations of species occurrence are not indicative of the true range of species adaptability or of the mechanisms than determine changes in species composition.

CHAPTER V

CONCLUSIONS

CHAPTER II

1. No statistical differences were observed in the seed germination of early and late seral dominant forbs or early and late seral grasses, but significant differences were observed in the responses of grasses and forbs. In general, seed germination of forb species was greater under light than dark conditions and following wet cold storage. The grass species had less specific seed germination requirements than the forbs.

2. To obtain maximum germination in reclamation efforts, seeds of the forb species should be sown at shallow soil depths in autumn. In contrast, adequate germination of the grass species could be obtained from either shallow seeding or drilling in autumn.

CHAPTER III

1. Differences between the late seral dominant forb and the early seral dominant grass in growth responses, response to N, and P and N uptake were consistent with predictions that relate species responses to nutrient levels as these change during succession. The late seral dominant forb responded like a species from a low-nutrient environment, exhibiting a much lower RGR and generally higher R/S

ratios than the early seral dominant species. In addition, the early seral dominant species showed a greater response to levels of N, while the late seral dominant species was more sensitive to levels of P.

2. Recommendations for revegetation methods to establish early and late seral dominants on disturbed sites include use of a 1:1 ratio of N and P, inclusion of late seral dominant species adapted to low nutrient conditions, and altering seeding densities to allow establishment of species with low RGRs.

CHAPTER IV

1. The effect of disturbance type on soil water, temperature, and nutrients were similar to those observed in more temperate ecosystems (Chapin 1983, Vitousek 1985). The highly-organic, dark-colored soils of the disturbed area had higher N and P levels and temperatures than the undeveloped loamy sand soils of the undisturbed area. No differences in soil water potential existed between the two disturbance types, but the vegetated undisturbed area had lower soil water potentials due to greater plant uptake late in both growing seasons.

2. Soil water potential did not limit seedling growth or survival on either of the disturbance types or on vegetated plots on the undisturbed area during the 1985 or 1986 growing seasons. In other alpine ecosystems soil drought that occurred late in the growing season was one of the primary causes of seedling mortality (Bonde 1968, Bliss 1971, Jolls and Bock 1983).

3. The higher levels of soil nutrients and warmer soil temperatures on the gap-type disturbance resulted in greater seedling growth and survival during 1986 than on either fertilized or nonfertilized plots of the severely disturbed area. Higher soil temperatures and levels of organic matter on the gap disturbance type may be conducive to greater rates of mineralization, and consequently, higher levels of available nutrients.

4. N and P fertilization resulted in generally higher seedling mortality, especially of ruderal species, despite greater seedling biomass. Fertilized plots experienced an initial pulse of N and P followed by a decline in N. The initial flush of nutrients resulted in greater plant biomass that may have created plant nutrient demands in excess of soil nutrient availability during the second growing season (Chapin 1980).

5. The growth responses of early and late seral dominant alpine species to N and P observed in the field differed from those measured in the greenhouse (Chapter III). Under greenhouse conditions R/R+S ratios decreased with increases in N and P. In contrast, no differences in R/R+S ratios were found between fertilized and nonfertilized plots in the field study. Factors other than N and P may be limiting under field conditions, e.g., soil temperatures.

6. On the severely disturbed area mulching had no effect on seedling growth, but often resulted in higher seedling emergence and survival. Mulch had almost no measured effect on soil water, temperature, or nutrients. However, wind both removed and redistributed mulch on treated plots. The resulting patchy

distribution of mulch may have created microsites favorable to seedling emergence and survival.

7. Few seedlings of either early or late seral dominants and no seedlings of ruderal species established on vegetated plots on the undisturbed area. Once seedlings established in vegetated plots, survival did not differ from that on cleared plots on the undisturbed area.

8. Species responses to differences in disturbance type and treatments varied and were, for the majority of comparisons, related to successional affinity. Seedling emergence of the large seeded late seral dominants, G. rossii and F. idahoensis, was benefitted more by mulching than that of the small seeded early seral dominants and the late seral dominant, A. scopulorum.

9. The early seral species, especially S. procumbens, exhibited delayed emergence of part of the seed population. These results are similar to those of the germination study of the same early and late seral dominant species under light or dark conditions following wet or dry cold storage (Chapter II). Delayed germination is often observed in annuals and may be a general adaptation of species with a high probability of failure (Cohen 1966).

10. The growth responses of the early and late seral species were consistent with predictions that relate species responses to successional stage (Grime 1977, Chapin 1980) and corresponded to the results of the greenhouse study that examined the response of D. cespitosa and G. rossii to N and P (Chapter III). Seedling growth was greater for the early seral dominants than for the late seral dominants when measured after two growing seasons. In addition, R/R+S

ratios were lower for early seral dominants, D. cespitosa and S. procumbens, than for the late seral dominants.

11. Survival of all of the species examined, except F. idahoensis, was generally high. Early and late seral dominants emerged and survived on the severe disturbance almost as well as on the gap disturbance type. Also, survival of early and late seral dominants and ruderals on mulched and fertilized plots on the severe disturbance was similar. This indicates a broader range of adaptability for these alpine species than is usually ascribed to species with different successional affinities.

12. Successional processes following disturbance in this alpine ecosystem appear to adhere to the initial floristics of Egler (1954) or the tolerance model of Connell and Slatyer (1977). Establishment of species with different successional affinities on disturbed alpine areas may depend upon two factors: 1. Species from varying successional stages have different seed production and dispersal characteristics. 2. Differences in particle sizes of the soil surface of disturbed areas determine the numbers and types of seeds that are "trapped" in the soil.

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APPENDIXES

APPENDIX A. CONSTRUCTION AND USE OF MAPPING TABLE USED FOR COLLECTING PLANT POPULATION DATA

Introduction

Researchers and managers alike are placing greater emphasis on understanding the life history characteristics of plants. Basic demographic data, including patterns of recruitment, reproduction, and survival, are central to understanding plant population dynamics. Such information, in combination with the proper correlative data, allows prediction of changes in plant populations in response to environment, competition, herbivory, or other factors (Schall 1984). Applied uses of these data are many and varied. For example, acquiring detailed life history information on rare and endangered plants can help managers devise strategies for insuring their preservation.

Mapping tables are routinely used for collecting plant demographic data (e.g., Mack and Pyke 1983, Mack and Harper 1977), but seldom is detailed methodology presented. I describe the construction and use of an acrylic mapping table designed for obtaining basic demographic information from plant populations. My primary objective was to design and construct a table that would allow accurate and precise relocation of mapping quadrats and plants using acetate sheets as "maps." The table was designed so that permanent mapping quadrats were relocated from the positions of permanent corner stakes marked on acetate sheets, rather than from fitting table legs over permanently set stakes. Because the angle of viewing influences the ability to

precisely relocate objects on the ground, the table was built so that its surface could be easily leveled on uneven ground. The mapping table had to be portable but sturdy enough to support a mapper leaning upon it and stable enough not to move during mapping.

Mapping table construction

My mapping table consisted of a sheet of 60 x 60 cm Plexiglas acrylic, 1 cm thick, mounted on two pieces of aluminum bar with attached leg supports (Fig. A.1). The dimensions of the mapping table can be adjusted to accommodate the desired mapping quadrat size, but the acrylic thickness should be at least 1 cm to provide the desired rigidity. The aluminum bars (2.5 x 1 cm) were 60 cm in length and were attached to opposing sides of the acrylic with counter-sunk bolts to provide a smooth table surface. To facilitate placement of the bolts, holes were drilled into the acrylic, and matching holes were threaded into the aluminum bars. Leg supports, consisting of 7.5 cm lengths of square aluminum tubing (2.5 x 2.5 cm with a 2.0 cm bore), were welded vertically onto each end of the aluminum bars. A small triangular brace made from a piece of aluminum bar was then welded between the tubing and the aluminum bars supporting the table to provide added strength. Wing-nut bolts mounted on the leg supports were used to position the legs at the desired height. Small pieces of aluminum bar, 2.5 cm^2, were affixed to the leg supports as reinforcement for the wing-nut bolts. Holes for the bolts were then threaded through both the base and the tubing of the leg support. The legs were 75 cm lengths of solid aluminum rod, 2 cm in diameter. To

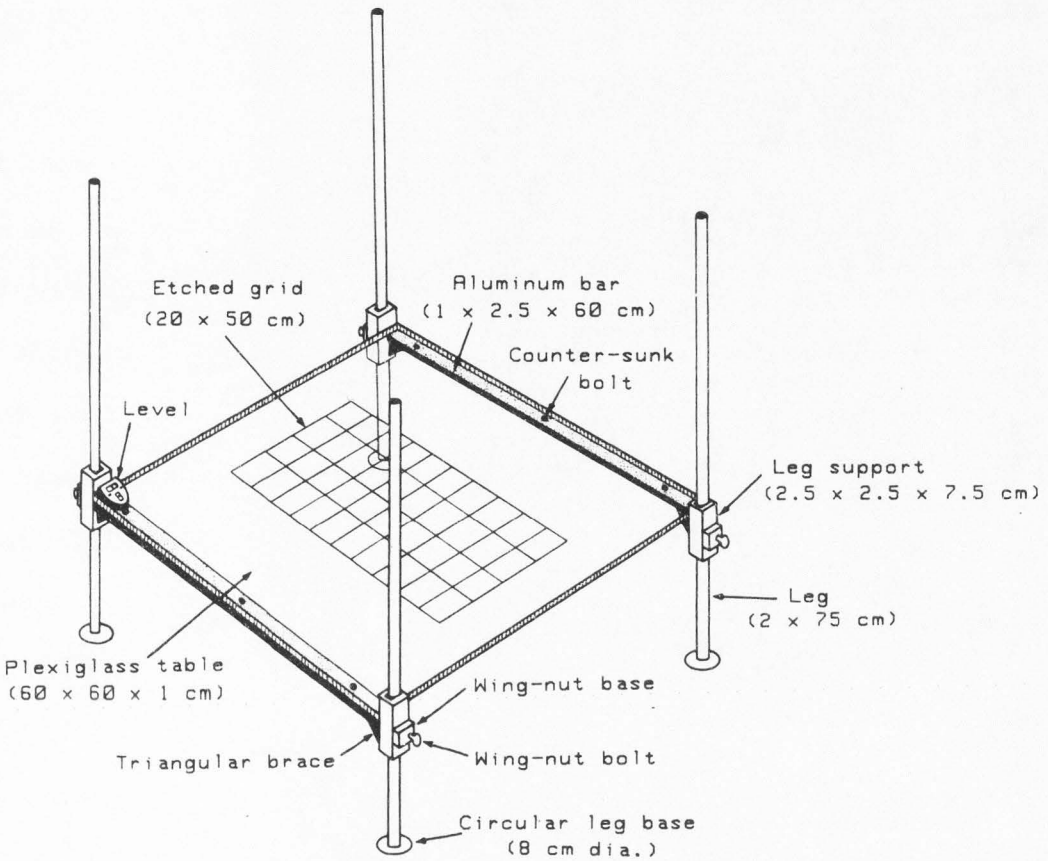

FIG. A.1. Detail of mapping table.

provide increased stability for the table, circular aluminum plates 8 cm in diameter were cut from 3 mm sheet aluminum and welded onto the legs.

A small carpenter's level with 2 bubbles at right angles to each other was mounted on the table surface for leveling. A mapping quadrat (20 x 50 cm) was then etched onto the bottom surface of the acrylic with a diamond stylus. The mapping quadrat was gridded using a 5 cm spacing to facilitate searching for plants.

A spotting device was constructed to enable precise relocation of stakes marking the mapping area and plants (Fig. A.2). The eye piece was a section of 5.4 cm diameter aluminum pipe (3.8 cm bore) with 2 sets of wire "cross-hairs" welded to a triangular base. Four sets of holes (0.51 mm), vertically spaced 4 cm apart, were drilled into the pipe at right angles for placement of the wire. The wire (chrome, 0.40 mm) was threaded through the holes and fastened in place with anchor screws. The base was constructed from a 0.5 cm aluminum sheet that measured 22.5 cm on each side, and that had a 3.8 cm hole drilled in the center for alignment with the pipe. The 3 legs were 1.3 cm aluminum pipe, 7.6 cm long, welded to the three corners of the triangular base. Rubber feet were fitted over the bottoms of the legs to prevent scratching of the table surface or acetate maps. An alternative spotting device consists of a piece of Plexiglas acrylic tubing with a slot cut in the base for marking pen access (Dave Pyke, personal communication). A piece of tubing approximately 10 cm in diameter and 15 cm in length with 2 sets of "cross-hairs" 4 cm apart would be adequate.

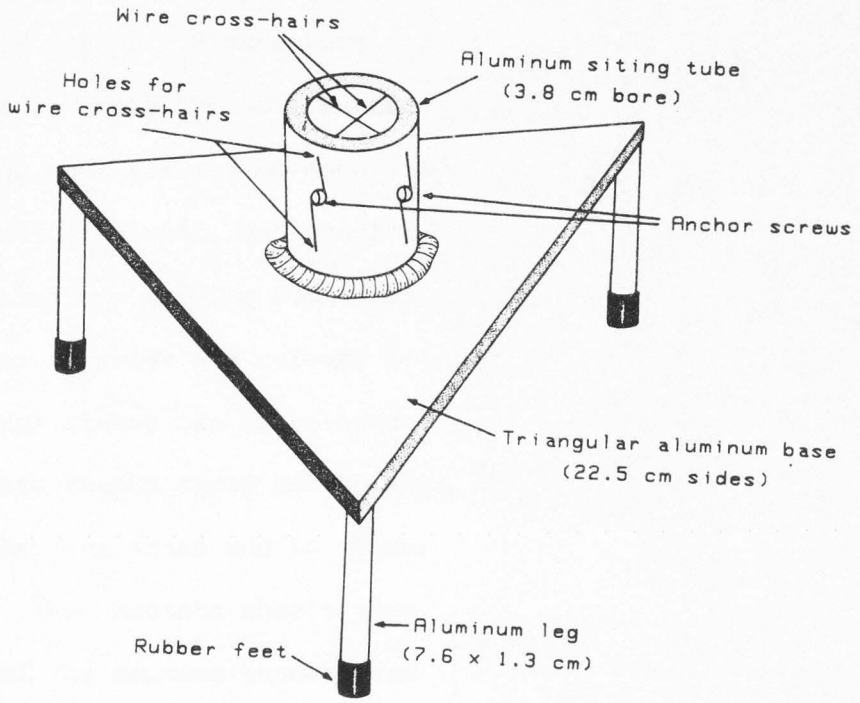

FIG. A.2. Spotting devise for alignment of stakes and plants.

Mapping table use

Repeated mapping of individual plants requires placing the table over permanent mapping area locations. Mapping area locations were marked on the ground with 3 metal stakes, 1 cm in diameter and 45 cm long, placed at 3 corners of the mapping area. Stakes were placed 5 cm outside of the mapping quadrat boundaries to minimize interference with the plant population. A template was used to insure accurate location of stakes. Stakes were driven into the ground so that about 5 cm extended above the soil surface. Metal "rebar" (concrete reinforcing rod) resists movement due to frost action when driven 35 to 40 cm into the soil, and provides inexpensive, permanent stakes. However, aluminum welding rod (3 mm dia.) will also resist frost heave and will not corrode and release undesirable metal compounds into the soil. Metal stakes can be relocated with a metal detector.

Acetate sheets taped to the mapping table surface were used to relocate mapping areas and to census populations within the mapping quadrats. The acetate sheets were cut large enough to include both the area of the mapping quadrat and the permanent stakes. The four corners of the mapping quadrat (not the stakes) were marked on acetate sheets, and these were taped over the mapping quadrat that was etched on the table.

Relocation of the mapping quadrat was solely dependent upon accurate positioning of the mapping table over the 3 permanent stakes delineating the mapping area. To insure exact positioning, the corners of the mapping table were adjusted so that the table surface was horizontally level. The exact positions of the stakes delineating

the mapping area were then located by aligning the "cross-hair" wires of the spotting device on the stakes. For the first mapping, the positions of the stakes were marked on the acetate sheets with permanent-ink marker pens while aligning the "cross-hair" wires on the stakes. During subsequent mappings, previously mapped acetate sheets were repositioned on the table, and the table was then moved until stake positions marked on the acetate sheets were exactly aligned with stakes in the ground.

Once the mapping table was precisely located over the mapping quadrat, plant populations were censused. The base of individuals were located using "cross-hair" wires on the spotting device and their status recorded on the acetate sheets. Different colors of marking pens and different symbols were used to record population data, such as introductions and deaths, and to differentiate sample dates and species.

The mapping table is probably best used in fairly low-growing vegetation or during the early phases of seedling establishment on disturbed or open areas. I used the mapping table in an alpine ecosystem during 2 growing seasons to record seedling survival under a variety of treatments. Seedling establishment within dense vegetation and beneath mulch was determined by reaching under the table and gently spreading the vegetation or lifting the mulch with a metal chaining stake. The mapping table could be used for recording other vegetation characteristics, including aerial or basal cover, vegetative establishment via rhizomes or stolons, and phenology. In addition, the table could be used for detailed mapping of soil surface characteristics, e.g., crytogamic crusts.

APPENDIX B. GENEARALIZED ANOVAs FOR SOIL TEMPERATURE AND WATER POTENTIAL DATA AND HARVEST BIOMASS DATA

Soil Temperature and Water Potential				Biomass	
Disturbed Area		Undisturbed Area		Disturbed Area	
Source of Variation	df	Source of Variation	df	Source of Variation	df
Year (Y)	1	Year (Y)	1	Year (Y)	1
Replicates (R)	2	Replicates (R)	2	Replicates (R)	2
YxR	2	YxR	2	YxR	2
Treatments (T)	4	Clearing (C)	1	Fertilizer (F)	1
Control vs. Rest	1	Seeding (S)	1	Mulch (M)	1
Among Rest	3	CxS	1	FxM	1
Fertilizer (F)	1	YxC	1	YxF	1
Mulch (M)	1	YxS	1	YxM	1
FxM	1	YxCxS	1	YxFxM	1
TxY	4	Error a	12	Error a	12
Error a	16	Depth (D)*	2	Species (S)	5
Depth (D)*	2	YxD	2	FxS	5
YxD	2	CxD	2	MxS	5
TxD	8	SxD	2	FxMxS	5
TxYxD	8	YxCxD	2	YxS	5
Error b	40	YxSxD	2	YxFxS	5
Period (P)	3	YxCxSxD	2	YxFxMxS	5
YxP	3	Error b	32	Error b	80
TxP	12	Period	3	TOTAL	143
TxYxP	12	Error c	6		
DxP	6	PxY	3		
YxDxP	6	PxC	3		
TxDxP	24	PxS	3		
TxYxDxP	24	PxCxS	3		
Error d	174	PxYxC	3		
TOTAL	359	PxYxS	3		
		PxYxCxS	3		
		PxD	6		
		PxYxC	6		
		PxCxD	6		
		PxSxP	6		
		PxYxCxD	6		
		PxYxSxD	6		
		PxCxSxD	6		
		PxYxCxSxD	6		
		Error d	138		
		TOTAL	287		

* df = 2 for soil water potential data; 1 for soil temperature data.

VITA

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OBJECTIVE

Research and professional advancement in the field of plant ecology. Special interests include: 1) alpine and desert ecosystems, 2) successional processes, nutrient dynamics and species diversity relationships, and 3) land reclamation.

EDUCATION

PH.D. in Biology-Ecology, Utah State University, Logan, Utah, 1987. Dissertation: Disturbed Alpine Ecosystems: Seedling Establishment of Early and Late Seral Dominants

M.S. in Range Science, Utah State University, Logan, Utah, 1979. Thesis: The Effects of Grazing on Salt Desert Shrub Species Survival During a Period of Below-average Precipitation

B.S. in Wildlife Conservation, Idaho State University, Pocatello, Idaho, 1975.

PROFESSIONAL EXPERIENCE

Range Scientist, GS-12, Intermountain Research Station, Forestry Sciences Laboratory, Logan, Utah, 1983 to present.

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Range Conservationist, GS-7/9, Boise District Office, Bureau of Land Management, 1979-1981.

Range Technician, Boise District Office, Bureau of Land Management, 1977.

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Secretary, Western Regional Coordinating Committee - 21 (Land Reclamation), 1986.

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Society for Range Management Annual Meeting, Calgary, Canada, 1982. "Naturally and artificially revegetated mined lands and adjacent natural areas in alpine ecosystems: a comparison."

High Altitude Revegetation Workshop, Fort Collins, CO, 1984. "Examination of plant successional stages in disturbed alpine ecosystems: a method of selecting revegetation species," (with R. W. Brown and R. S. Johnston).

Society for Range Manangement Annual Meeting, Salt Lake City, UT, 1985. "Response of an early successional alpine grass and a late successional alpine forb to N and P availability: implications for revegetation, " (with J. A. MacMahon and R. W. Brown).

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